

THE INFLUENCE OF MATING SYSTEM AND DISPERSAL PATTERNS  
ON THE GENETIC STRUCTURE OF RED HOWLER MONKEY POPULATIONS

By

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To my parents

Mary and Edward

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By

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The relationship between social structure and partitioning of genetic variance was examined in a red howler monkey (Alouatta seniculus) population in Venezuela. Dispersal patterns and breeding structure were determined through long-term censusing of troops, and radio-telemetry and activity budget data on solitary migrants. Standard electrophoresis techniques were used to examine 29 loci in blood samples taken from 137 of the study animals. Analysis of the genetic variance within the population demonstrated (1) an excess of heterozygosity within troops relative to that expected by classical variance components predictions ( $F_{IS} < 0$ ) and (2) a high level of genetic variation among troops ( $F_{ST} = 0.216$ ). These conditions are maintained and promoted by the accumulation of relatedness among troop females, a single-male harem breeding structure, and a low rate of random exchange of breeding males.

Relatively high levels of heterozygosity ( $H = 0.11$ ) are thus maintained despite population subdivision into small, socially isolated "demes" (troops) with less than one immigrant per generation. Individual troops can exhibit gene frequencies at various loci that diverge widely from the frequencies observed in the rest of the population. Interdemic selection in such a mosaic of genetic variation could result in the more rapid spread of advantageous gene combinations than in a panmictic population, particularly in a colonizing situation. The rapid local adaptation made possible by these factors may have helped to promote the tremendous radiation that was responsible for the current range of the genus Alouatta.

## CHAPTER 1 INTRODUCTION

The manner in which social organization influences the genetic structure of a population will have important consequences for the flexibility with which it can respond to environmental change. Effective population size, dispersal patterns, and mating system can influence the maintenance of gene diversity within the population, and the proportion of the genome exposed to selection (Wright 1946, 1965, 1980; Slatkin 1976). The manner in which this influence operates is poorly understood, and is confined largely to predictions based on theoretical treatments. Few demography studies have been able to determine rates of gene flow among the different substrata of socially structured demes, and fewer still have been able to correlate this information with genetic data on the populations being studied (see Chepko-Sade et al. 1987 for a review). Results from studies examining the genetic structure of socially subdivided populations have been contradictory, and difficult to compare due to lack of agreement on the appropriate level of resolution (i.e., is the smallest population subunit a coterie, a ward, a colony?). Although variable amounts of genetic heterogeneity among social units have been demonstrated in these studies, the degree of genetic divergence predicted by classic isolation model theory has not been consistent with presumed rates of gene flow

(see Chapter 4). The mechanism whereby genetic diversity is maintained in these populations remains unclear.

This study documents breeding structure and patterns of dispersal among social groups in the red howler monkey (Alouatta seniculus), and correlates these findings with data on the genetic structure exhibited within and between populations. The red howler monkey is one of the most widely studied of the New World primates, and various aspects of its social system have already been described in numerous publications (see Crockett and Eisenberg 1987 for a review). Range in troop size and composition remains consistent throughout their geographic range, but the breeding structure appears to be highly plastic. Males aggressively defend groups of females from other males either alone, or in cooperative alliances that may endure for years. Females may disperse or remain in their natal troop to breed. The proportion of animals in the population exhibiting each of these strategies varies in different areas and may be related to differences in habitat and population density (Crockett 1984, 1985). Correlation of genetic variance with intraspecific variation in reproductive tactics of this type was potentially useful as a test of the underlying mechanisms of cause and effect.

In the chapters that follow: (1) variance in male reproductive success within troops is determined through paternity exclusion with genetic markers, and used to examine the trade-off between the costs and benefits of male cooperation among relatives and non-relatives; (2) the influence of resource distribution on differences in male and female dispersal patterns is investigated. Rates of gene flow between

populations, and among troops within populations, are described; (3) partitioning of genetic variance among troops within and between populations is determined based on ten variable loci, and these results are compared to those predicted by isolation model theory from observed rates of gene flow. Correlation of genetic distance with geographic distance is examined. Finally, models describing the influence of social organization on rates of evolutionary change are evaluated based on these findings.



CHAPTER 2  
THE REPRODUCTIVE CONSEQUENCES OF MALE COOPERATION:  
PATERNITY EXCLUSION IN MULTI-MALE AND SINGLE-MALE TROOPS  
USING GENETIC MARKERS

Introduction

Cooperation among males in obtaining and defending access to reproductive females has been reported in a wide variety of vertebrate breeding systems (e.g., lions, Bygott et al. 1979; Native Hens, Ridpath 1972; baboons, Smuts 1985). The relative contributions of direct and indirect selection to the evolution of such coalitions have been difficult to distinguish. The reproductive trade-offs for each participant will depend on (1) the extent to which mating is shared among coalition members, and (2) the advantage that each individual in the coalition gains over competing alone. In many, perhaps most, species exhibiting this type of male cooperation, males compete as both single individuals and as coalitions (e.g., Brown 1987, p.134; Smuts 1987), such that the decision to join a coalition is only one of several alternative reproductive strategies.

The reproductive costs and benefits of male cooperation are examined here in the red howler monkey. Red howler males appear to be able to adopt a variety of reproductive tactics. Various aspects of the breeding system have been described by Rudran (1979), Crockett (1984), Crockett and Sekulic (1984), Crockett and Eisenberg (1987), and Sekulic

(1981, 1983). Troop composition may be single-male, age-graded male, or multi-male. Males form coalitions of two to four individuals that aggressively invade bisexual troops and attempt to evict resident males. Once membership in a troop has been established, they may then continue to cooperatively defend the troop against other such invasions, or one or more of them may emigrate. The manner in which these coalitions form is highly variable and may consist of either related or unrelated individuals. In multi-male troops, the dominant male appears to perform most of the copulations. Infanticide by immigrant males may occur during and after an invasion and after status changes between troop males.

This study examines variance in male reproductive success in single and multi-male red howler troops through paternity exclusion using genetic markers. The influence of inclusive fitness is assessed by comparing coalitions of relatives to coalitions of non-relatives with regard to duration time, stability, and number of offspring expected for each participant based on the paternity exclusion results. Finally, the population context in which cooperation tends to occur is described, and the consequences of non-cooperation explored for both dominant and subordinate individuals.

#### Methods

The study area was Hato Masaguaral, a wildlife preserve in the central llanos of Venezuela that has been described in numerous publications (e.g., Rudran 1979; Troth 1979; Crockett 1985). The population of red howlers that occupies the shrub woodland habitat in the western portion of the preserve was censused by Neville in 1969

(Neville 1972), by Eisenberg and Kleiman in 1975 (Eisenberg, pers. comm.), by Rudran in June and July of 1976, and from January 1977 through October 1978 (Rudran 1979), by Crockett from March 1979 through February 1981, and in February 1983 (Crockett 1985), and by the author throughout 1981, 1984, and the first seven months of 1985. The number of troops censused grew from 14 in 1975 (Eisenberg, pers. comm.) to 33 in 1985 as additional troops were discovered at the periphery of the study area, or were newly formed within.

#### Distribution of Paternity Among Troop Males

The techniques used for capturing animals from the study population were originally developed by Scott et al. (1976), and are reported in detail by Thorington et al. (1978). In December and January of 1981, individual howlers were immobilized using a CO<sub>2</sub> rifle loaded with Pneu-darts containing Phencyclidine in a dose of approximately 10 to 20 mg/kg body weight. Drugged animals were caught in hammocks as they fell to the ground, after which they were kept sedated with Ketamine HCl administered as needed in doses of 20 mg/kg. Blood samples drawn from the femoral artery were separated into serum and hemolysate components and frozen in liquid nitrogen, where they were stored until laboratory analysis. Animals were allowed to recover and were then released at the location where they were captured.

Samples were collected from 137 animals representing four multi-male troops and five single-male troops in which there had been no changes in male tenure for at least two years. Two additional troops were sampled in which one of the two males that had previously occupied the troop had emigrated during the year prior to sampling. Whole troops

were captured whenever possible. Offspring born prior to the last male tenure change in their troop could not have been fathered by any male in the troop at the time of sampling and were omitted from the paternity exclusion analysis. Mother-offspring genealogies were known based on the five years of troop census data previous to the sampling period. Standard starch gel and polyacrylamide techniques were used to examine 29 loci. Buffer systems and staining procedures were those described by Harris and Hopkinson (1976), unless otherwise noted. Ten loci were polymorphic: phosphogluconate dehydrogenase (6PGD), purine nucleoside phosphorylase (PNP), adenylate kinase-1 (AK-1), adenosine deaminase (ADA), glucose phosphate isomerase (GPI), peptidase C (PEP C), peptidase D (PEP D), malic enzyme (ME; Selander et al. 1971), transferrin (Tf; Altland et al. 1981; McClellan 1982), and an unidentified serum protein (SER-1) that ran consistently one-half way between the origin and the transferrin band on a standard Tris/HCl polyacrylamide gel, pH 8.6 (McClellan 1982), stained with Coomassie Brilliant Blue in 3.5% perchloric acid (Reisner et al. 1975). Details of gel running procedures and information on non-variable loci are described in Chapter 4. Variation at the transferrin locus was significantly correlated with sex and was therefore not useful for paternity analyses. The nine remaining variable loci were used as genetic markers to examine paternity in the 11 troops that were sampled.

All adult males present in a troop at the time of conception of a given troop offspring were considered to be possible fathers. A male was excluded from paternity if he did not have at least one allele in common with the offspring in question at every locus. In multi-male

troops, the probability of getting the observed distribution of paternity if all troop males have equal probability of fathering offspring was tested using a randomized block design for correlated proportions and applying Yates correction for small sample size (Sokal and Rolf 1969; pp. 610-17). The possibility of offspring being fathered by males living outside of established troops was examined by testing for evidence of outside male paternity in the five single male troops that were captured. These results were supplemented by long-term observations of male and female behavior within troops when a female comes into estrous. Troops in the study population were observed throughout 1981, 1984, and the first half of 1985 during the course of extensive activity budget sampling and censusing (c.f., Chapter 3).

#### Relationship Between Origin and Duration of Male Coalitions

A male coalition was defined as any combination of two or more adult or subadult males that co-inhabited a bisexual troop for a minimum of one month together, during which time they maintained exclusive access to troop females by cooperatively preventing other males from entering the troop territory. Male coalitions were classified according to their origin and duration based on the 1981-85 census data and on written accounts of male coalitions that occurred during the four years of population observation preceding that period (Crockett and Sekulic 1984; Rudran 1979; Sekulic 1981, 1983). The majority of male coalitions described in these studies were of unknown origin due to the difficulty prior to 1981 of identifying young males after dispersal (Crockett 1984), and to the fact that a large proportion of the coalitions in the population were already formed before Rudran's first census in 1976

(Rudran 1979). While identification of coalitions of relatives was usually not feasible during this period, characterization of coalitions based on whether the individuals emigrated from the same troop together or whether they originated in different troops was frequently possible (e.g., troop IV, Rudran 1979; troop M74, Sekulic 1981; troop M71, Crockett and Sekulic 1984). During the 1981 capture procedure described above, 175 howlers were marked with unique patterns of colored ear tags that permitted positive identification of individuals after dispersal (see Chapter 3 for details). The genealogical relationships among natal troop males were by this time known for most troops in the population. These two factors facilitated more frequent identification of the genetic relationship between males that subsequently formed coalitions.

Male coalitions of known origin were classified into two categories:

(1) Males were relatives or had a high potential of being relatives: Males in coalitions were known relatives (father and son, brothers, or half brothers) or had emigrated together from the same troop and successfully invaded another troop.

(2) Males were not relatives or had little potential of being relatives: Males in coalitions were born in different troops or did not occupy the same troop together when first encountered in the study population. Either both originally occupied different troops within the study area, or one occupied a troop within the study area while the other came from outside the population, origin unknown. All coalitions in the population for which this information was known were used ( $n = 32$ ). Since the complete survival time of all coalitions was not known,

the mean duration of association within each of these categories was calculated using a clinical life table analysis of survivorship in which coalitions could enter the study at any time and be withdrawn prior to their termination (Peto et al. 1976). Any coalition in which the participants separated prior to the end of the study period was considered a termination. Those coalitions that were still ongoing at the end of the study period were classified as withdrawals. Mean life expectancy of coalitions was calculated as  $e(x)$ . Duration of the two types of coalitions was compared using the logrank test for statistical comparison of life tables (Peto et al. 1977).

### Results

#### Distribution of Paternity

In the five single male troops that were examined, there was no evidence that males living outside of the troop had fathered offspring by troop females (Table 1). One of the single male troops (M78) had been occupied for 1.25 years by another adult male, who entered the troop in June 1978 and left in October 1979 (Crockett and Sekulic 1984). The resident adult male was excluded from fathering one of the offspring conceived in the troop during this period. He could not be excluded from fathering any of the offspring conceived in the troop before or after this interval. In no other case could the resident adult male in a single male troop be excluded from fathering offspring born into the troop during his tenure.

Table 1. Paternity exclusion results for multi-male and single-male troops. Probability that paternity is distributed equally among males in a multi-male troop is less than 0.001 ( $p < .001$ ).

#### A. Multi-male Troops

Troop	Male	# Offspring Excluded	# Offspring Assigned	# Offspring Inconclusive
M61	33	4	0	
	6	0	4	1
M64	5	3	0	
	3	0	3	0
G20	138	3	0	
	137	0	3	0
M62	2	0	2	
	5	2	0	
	3	3	0	1

#### B. Single-male Troops

Troop	Male	# Offspring Excluded	# Offspring Assigned	Inconclusive
M52	128	0	4	0
M57	1	0	2	0
M78	35	0	4	1*
M79	157	0	4	0
G21	76	0	2	0

\* Male 35 excluded from fathering a single offspring conceived during a year when he co-inhabited the troop with another adult male (see text).



Observation data support this conclusion. No incidences of an adult troop female copulating or consorting with a male outside the troop were observed. Troops were small and cohesive, and rarely spread out in a manner that would allow such activities to occur without being observed by the resident male. Since infanticide and attempted infanticide commonly occurred after adult male replacement as well as during attempted troop take-over (Crockett and Sekulic 1984; Rudran 1979; Sekulic 1981, 1983), outside males were potentially reproductively detrimental to a troop female. Females participated with other troop members in threatening and howling at extra-troop males that approached the boundaries of the troop home range area.

The paternity exclusion results for the four multi-male troops are presented in Table 1. Based on the above evidence, it was assumed that resident males fathered all offspring born into the troop during their tenure, such that the male that could not be excluded was assumed to be the father of the offspring in question.

Troop M61. Four of the five sampled offspring could be assigned to male 6, while neither male could be excluded from fathering the fifth. Male 6 was the only male observed to mount troop females. Males 6 and 33 were both resident in troop M61 when Rudran first contacted the troop in 1976 and remained there until the end of the 1985 study period.

Troop M64. All three offspring could be assigned to male 3, who was observed consorting with troop females in June 1979 shortly after he and male 5 invaded M64 (Crockett, pers. comm). Male 3 was the only male observed to mount troop females after the 1981 sample and remained the apparent alpha male until the end of the 1985 study period.

Troop G20. All three sampled offspring could be assigned to male 137. No copulations were observed in this troop, which was outside of the woodland study area. Males 137 and 138 were resident in G20 when Crockett first contacted the troop in February 1980 and were still present until at least 1983 (Crockett, pers. comm.).

Troop M62. Three males were present in this troop when it was first contacted by Rudran in 1976. Between November 1978 and March 1979, males 3 and 5 left M62 and successfully invaded neighboring troop M64, leaving male 2 as the only resident male in M62. Three offspring were conceived prior to this event. Male 3 could be excluded from fathering all three, and male 5 could be excluded from fathering two of the three. Neither male 2 nor 5 could be excluded from fathering the third offspring. Male 5 was observed to mount a troop female in 1978 and to displace male 3 when he followed the female (Mack 1979, unpub. ms.). This relationship apparently reversed when these two males later invaded M64. Male 2 was classified as a subadult in 1976 but was seen mounting females in 1978 (Rudran, pers. comm.). Male 2 was almost certainly born in M62, since he and an old adult female in the troop were the only two animals in the population that carried the mutant SER1-150 allele at that time. His daughter born in 1980 also carried the allele.

In all cases, all but one male in the troop could be excluded from fathering all or most of the sampled troop offspring. In three of the troops, these were the males that were also observed to mount troop females. The probability of observing these results if all males had equal probability of paternity was less than .001 ( $\chi^2 = 8.1$ ,  $df = 1$ ). Relative aging of males based on alginat tooth casts taken at the time

of capture indicated that the putative father of the majority of troop offspring was in all four cases the youngest male (R. Thorington, pers. comm.).

Red howler troop females exhibit asynchronous breeding, such that only one of the two to four females that occupied a troop was likely to be in estrus at any one time (Crockett and Rudran 1987). This facilitated monopolization of estrous females by a single male. When a female came into estrous in multi-male troops, the apparent dominant male was observed to guard her closely, rarely straying more than 2 meters from her at any time. Other troop males were threatened when they approached with a chin thrust or lunge.

Female estrus was observed in three multi-male groups. In both troops M61 and M64 the male coalitions had lasted a minimum of nine years each and appeared stable: no status changes were observed in M61, and the status change between the males in M64 had occurred 6 years earlier. The subordinate male's attempts to approach an estrous female were easily discouraged by the dominant male in the manner described above during my 1984 observations. In both cases the dominant male was able to mate with the female repeatedly and without interruption while the subordinate male reclined at some distance, showing no apparent interest in the breeding pair.

The male coalition in troop M75 had lasted for 2.5 years when female estrus within the troop was observed. The apparent dominant male was repeatedly challenged by the subordinate male, such that the dominant male rarely had the opportunity to mount the female. When he did accomplish a mount, the subordinate male harassed the female by

touching her or by reclining in front of her in a grooming solicitation posture. The female did not conceive during that estrus. Although the subordinate male was never observed to mount the female, he effectively prevented the dominant male from successfully mating with her. One year later, the subordinate male emigrated from the troop. In cases wherein the status of the two males was in a state of conflict or transition, physical injury resulting from observed or implied aggression was observed frequently when troop females came into estrus (Crockett and Sekulic 1984; Sekulic 1983).

Status changes between coalition males, in which the formerly subordinate male succeeds in becoming dominant, as described above for coalition males 3 and 5, have been extensively documented by Sekulic (1981, 1983), and Crockett and Sekulic (1984), and were observed by the author in three additional cases. In the two troops sampled in which one of the resident males had recently emigrated, the remaining male could be excluded from fathering at least one of the offspring conceived during a time when the absent male had been considered dominant:

M63. Males 6311 and 6312 entered M63 in 1977 (Rudran 1979), at which time 6312 was considered a subadult. The trajectory of these two males' relationship is described by Crockett and Sekulic (1984) and by Mack (1979, unpubl. ms.). Male 6311 was considered to be dominant until mid-1978, during which time conflict followed by a status change occurred between the two males. By October 1978, male 6312 was dominant. Male 6311 became increasingly peripheral and left the troop in mid-1980. Male 6312 was excluded from fathering the offspring born in February 1978, just prior to his ascension to dominance, but could

not be excluded from fathering the four offspring born in April, September, and October of 1979, and June 1980 (Table 2).

M73. Male 7112 invaded troop M71 in 1977 and began to co-inhabit the troop with already resident male 7111. This event was followed by an infanticide (Rudran 1979). No other information is available on this male relationship during 1977, 1978, or the first part of 1979. Shortly after Sekulic began observing the troop in September 1979, male 7111 killed a new infant and mated with the mother when she came into estrus eight days later (Sekulic 1983). Male 7111 maintained a tenuous dominance throughout Sekulic's 1979 and 1980 observations, during which time multiple agonistic interactions took place between both males, but only 7111 was observed to mount females. Male 7112 emigrated from the troop in March 1980, approximately three years after he had joined it. Male 7111 was excluded from fathering an offspring born in September 1978, but could not be excluded from fathering offspring born in February and May of 1980 (Table 2). These data, in conjunction with the infanticide committed by 7111 in late 1979, suggest that 7112 was reproductively dominant for some period of time that ended shortly before Sekulic's study.

In those male coalitions characterized by conflict and status change, the male fathering offspring was thus subject to change as dominance changed. This occurred in troops M63, M71, and probably M78 during the time that it was briefly co-inhabited by an additional male. In each instance the losing male emigrated shortly after being supplanted, such that these cases were genetically equivalent to male replacement through invasion: the reproductive tenure of one male was

Table 2. Distribution of paternity between males within troops before and after status change.

# Offspring Assigned / # Sampled			
Troop	Male	Before Status Change	After Status Change
M63	6311	1/1	0/4
	6312	0/1	4/4
M71	7112	1/1	0/2
	7111	0/1	2/2

followed by that of another. At any one period in time only one male appeared to sire troop offspring, and in all cases in which data are available this was also the male observed to monopolize reproductive access to females. This pattern was also observed in those multi-male troops in which male coalitions were apparently stable and of long duration: M61, M64, and G20.

#### Origin and Duration of Male Tenure

Male coalitions of relatives and potential relatives had a mean survivorship of 8.2 years. This was significantly higher than the mean survivorship of 2.3 years observed for coalitions in which males had little or no potential of being related ( $\chi^2 = 8.89$ ,  $p < .001$ ). Regression of log transformed data points was used to fit survivorship curves of the form  $y = ae^{bx}$ ; and these are shown in Figure 1. Coalitions in the first category included five father-son pairs, three pairs of full sibs, one pair of half sibs, one quartet of combined sibs and half sibs, and four associations of males that emigrated from the same troop together ( $n = 14$ ). Non-relative coalitions included eight cases of single male troops that were joined by single outside males who then co-inhabited the troop with the resident (e.g., M71, M78), seven cases in which one male came from a troop in the population and the other came from outside, and three cases in which the males came from different troops ( $n = 18$ ).

In addition to lasting longer, male coalitions among relatives and potential relatives appeared to be more stable than coalitions among non-relatives (Table 3). Status changes occurred in 7 of the 18 non-relative coalitions, and in 6 of these cases the losing male

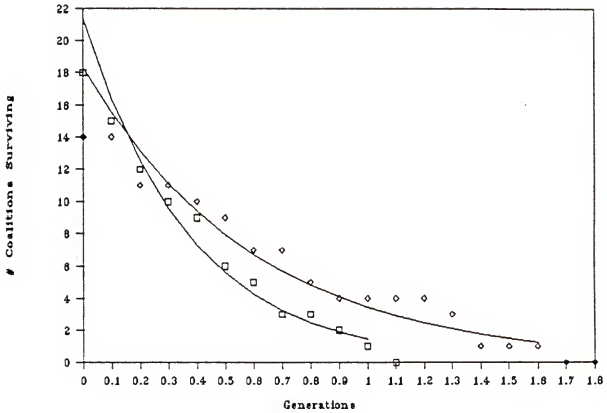


Figure 1. Comparative survivorship of coalitions of related versus unrelated males. One generation equals five years.  $\diamond$  : males related;  $\square$  : males unrelated.



Table 3. Duration and stability of male coalitions between related males compared to those between unrelated males.

	Male Coalitions	
	Related	Unrelated
n	14	18
Mean Duration	8.2 years	2.3 years
# Status Changes	3	7
Terminations:		
Beta-male Leaves	1	14
Other	5	2

emigrated within one year or less. In the seventh case (M71, see below), the losing male remained in the troop until he was able to regain his original breeding status. Seven of the remaining non-relative coalitions also ended when the male who appeared to be reproductively subordinate emigrated, as in the case of M75 described above.

Status changes occurred in three of the coalitions between relatives/potential relatives. Unlike the former category, however, the deposed male did not emigrate, and the coalition continued:

(1) In the case of M64 described above, male 5 was still with male 3 at the end of the 1985 study period, seven years after the apparent status reversal between them. Male 5 was approximately ten years older than male 3, based on toothwear (R. Thorington, pers. comm.), and was possibly male 3's father.

(2) In troop M54, natal male 5431 gained dominance over male 30 by February of 1984. Both males were still together in mid-1985. Male 5431 was approximately one year old when M54 was first contacted in 1977, while male 30 was the only adult male present in the troop at the time and was therefore considered to be 5431's father. Male 5431 reached adulthood in 1981.

(3) Males 19 and 20 emigrated together from troop M73 in March 1978 and successfully invaded neighboring troop M74 (Rudran 1979, Thorington et al. 1979). They remained together until sometime between February 1983 and February 1984, three to four years after a brief status change in 1979 that was reversed seven months later (Crockett and Sekulic 1984; Sekulic 1983).

Anecdotal evidence suggests that males choose relatives over non-relatives as partners when possible:

(1) Troop M71 was invaded in 1980 by young adult male 8 from adjacent troop M72, who co-inhabited M71 with resident adult male 11 for the next four years. By early 1984, two of male 11's sons had reached subadult age. In March 1984 male 11 and his sons collectively evicted male 8 from the troop, who was last seen in the population being chased by the two subadult males.

(2) Troop M63 was invaded by male 24 in 1976 along with three other incursive males, at which time male 26 was a large juvenile presumably born into the troop (Rudran 1979). By mid-1980, male 24 was the only one of the invading males that remained in the troop, and male 26 had reached adult age. When male 26 began in 1981 to spend time away from the troop in a manner typical of young males just prior to emigration (see Chapter 3), male 26 actively sought him out. Male 24 had been occupying a peripheral part of the troop home range for three days when male 26 approached him there and touched his arm. Male 24 lunged at him, but male 26 approached a second time. After a brief head-bobbing session, they play-grappled for several minutes. They rested next to each other for an hour and remained within close proximity to each other for the rest of the day. Male 24 remained in the troop for four more years. This behavior suggests that the older male was an active rather than passive participant in establishing a coalition with the younger male, who's departure would have left male 26 as the only adult male in the troop. However, one month after male 26's son reached subadult age in 1984, male 24 emigrated completely. He was observed several months

later as a solitary extra-troop animal, and by the end of the 1985 study period he had still not become a member of an established troop.

#### Discussion

In multi-male red howler troops, only the dominant male was found to father offspring conceived during his tenure. In those cases in which observation data were available, this was the only male observed to mount females. The ability of a single male to monopolize breeding access to troop females was facilitated by non-synchronous estrous cycles among the two to five adult females that typically occupy a troop.

Red howlers are the only multi-male harem species that has been examined in which dominant status has been found to promote such a high degree of variance in male reproductive success within social groups. While numerous studies of Old World terrestrial primates have examined the effects of rank on mating success based on copulation rates (e.g., Hausfater 1975; Loy 1971; Struhsaker 1967) and on paternity exclusion in captive populations (Duvall et al. 1976; Smith 1981), in none of these studies was dominant status demonstrated to confer exclusive access to troop females. The relatively large troop size typically exhibited by these species would seem to preclude the possibility of a single male being able to monopolize access to all females. Lions have a breeding system very similar to that exhibited by red howlers except that lion pride females frequently come into estrus simultaneously (Packer and Pusey 1983). Although large lion males in their prime are sometimes able to displace weaker males (Packer and Pusey 1982), any male in the

pride may form a consortship with an estrous female (Bygott et al. 1979).

Among howlers, the only manner in which reproductive females could be obtained was through establishing membership in a bisexual troop. This was accomplished through aggressive invasion followed by replacement of the resident troop male(s) or by formation of a coalition with the resident troop male after invasion. Groups of migrant females without a territory were also sometimes defended by males, but unless a territory could be established, these females remained non-reproductive (see Chapter 3). Males attempting to form new troops in this manner were also subject to aggressive replacement. The intensity of competition during such events was evident in the incidence of injuries that were incurred during observed or inferred male physical aggression. Invasion attempts frequently resulted in severe injury to one or more of the opponents that was often debilitating and sometimes resulted in death (Crockett and Pope 1988). Such injuries commonly included amputated digits, broken limbs, loss of teeth, lips that were completely severed to beneath the eye, and lacerations in the head and groin area.

If competition for membership in a bisexual troop is the only manner in which access to reproductive females is possible, then joining a coalition will become a necessary pre-requisite to reproduction as the number of bisexual troops in the population that are multi-male and age-graded male increases. In 1981, half of the 26 troops in the population contained more than one fully adult male, and 12 of the remaining 13 had at least one subadult male (age-graded male troops), leaving only 1 truly single-male troop in the population. By 1984, the

number of troops being censused had grown to 34, and the number of multi-male troops to 22, or two-thirds of the total census population. Seven of the remaining 12 were age-graded male and 5 were single-male.

The number of subadult and large juvenile males retained in troops with only one fully adult male (age-graded and single-male troops) was significantly higher than the number retained in multi-male troops for all years between 1977 and 1985 except 1984 ( $p < .05$ , Mann Whitney U; Pope and Crockett, in prep). Subadult males were active and effective participants in both troop defense and invasion, and had the highest physical injury rate of any age-sex class in the population (Crockett and Pope 1988). The mean weight of subadult males was five-sixths that of adult males, and variances of both groups overlapped such that some subadult males were as large or larger than some adults (see Chapter 3).

A direct advantage of forming a coalition for both dominant and subordinate red howler males resulted from the superior competitive ability of coalitions over single males in establishing and maintaining tenure in the limited number of female troops in the population. No case of a single male being able to invade a multi-male or age-graded male troop was ever observed. Thus the number of troops in the population that a single male would be able to invade without help in any year was very small. The mean number of adult females per troop ranged between 2.7 and 2.9 throughout 1975 to 1984 (Crockett and Eisenberg 1987). Since a drop in troop sex ratio below one adult or subadult male to two adult females was always followed by successful invasion within a maximum of one year, usually much less (Pope and

Crockett, in prep), male cooperation was required in order to maintain tenure within a troop as well.

The ability of a male or coalition of males to defend a troop of females from other males was aided by the cohesiveness and intense territoriality displayed by troop females. Females participated vigorously in defending territory boundaries from surrounding troops, extra-troop males, and particularly extra-troop females, who were frequently chased and invariably bitten if caught (Crockett and Pope 1988; Sekulic 1982). Females also behaved aggressively towards natal females other than their own daughters, 72% of which emigrated before they reached reproductive maturity (Crockett 1984; c.f, Chapter 3). After emigration, extratroop females were aggressively excluded from immigration into other bisexual troops by troop females. They were able to reproduce by forming associations with other extratroop individuals only if the group could successfully defend a territory in a suitable area of habitat. This, however, was a relatively rare occurrence in the woodland study population (see Chapter 3). Extra-troop females without a territory were never observed to reproduce successfully. Their diets were significantly lower in both protein and phosphorus than those of troop females (see Chapter 3). These nutrients are typically limiting to reproduction in female herbivores (Lloyd et al. 1978), suggesting that extra-troop females may have difficulty obtaining adequate nutrients for gestation and lactation. Reproductive females, therefore, were grouped into small, spatially discrete clusters that could be effectively defended by males as a resource.

Although the mating success of a subordinate male in a coalition appears to be extremely low, his chances of establishing and maintaining membership in a bisexual troop as a single male may be even lower. A subordinate male in a coalition may have more breeding opportunities than a solitary, extra-troop male. The subordinate may eventually be able to assume dominance, particularly if he is a subadult and can expect to grow larger. He will be in a better position than an extra-troop male to know his potential adversary in terms of such attributes as size, strength, and experience, and should be better able to assess when choosing to engage in an encounter will be to his advantage. The relatively short duration of coalitions among non-relatives suggests that after some critical period of time in which no mating success has been achieved, the subordinate male may give up and try elsewhere. He is also in a better position than an extratroop male to take advantage of potential invasion opportunities when they arise in surrounding troops, such as the dispersal of a natal subadult male. The majority of all successful invasions that occurred between 1976 and 1985 involved the immigration of males from an immediately adjacent troop (see Chapter 3).

Occasionally, more than one female in a troop may come into estrus at the same time, particularly in those troops with four or more adult females (Crockett and Rudran 1987). Since guarding more than one female at a time in the manner previously described would be difficult for the dominant male, the subordinate male may be able to successfully copulate in such instances. Females, however, may avoid mating with subordinate males under these circumstances in order to avoid promoting conflict



among troop males that could result in infanticide. Infants conceived during both successful and attempted status changes among troop males have been subject to observed and inferred infanticide, as well as infants that were present when the disputes took place (Crockett and Sekulic 1984; Sekulic 1983). It may therefore be to a female's reproductive detriment to promote conflict in an otherwise stable situation by choosing to mate with a subordinate male once the dominance relationship has been established.

In cases wherein the adult males are related, the subordinate male will further benefit from inclusive fitness, the extent of which depending on the degree of relatedness between the males involved. In a population in which forming a coalition with another male is reproductively beneficial, a male should choose to form a coalition with a relative over a non-relative whenever possible. The small size of a red howler troop, in conjunction with long and staggered interbirth intervals, may preclude this possibility much of the time. The opportunity for a young male to leave his natal troop with another young male of comparable age should increase as troop size goes up, however, and thus coincide with those population conditions that favor male coalitions. Half of the coalitions between known relatives were between brothers or half brothers.

The intense competition for limited female troops may be responsible for the delayed dispersal observed among subadult and young adult males in age-graded male troops that would otherwise have been single male. Many males remained in their natal troops well into adulthood (see Chapter 3; see also below). When the likelihood of

obtaining reproductive status in a bisexual troop after dispersal is low, a young male may increase his fitness more by helping his father to produce full and half siblings than by trying to reproduce on his own. This would be especially true in those cases wherein the father would be left as the only male, thereby reducing his chances of being able to maintain tenure. In troop M71, for example, two subadult males left the troop in May 1985, leaving their father as the only adult male. By that afternoon, the troop had been invaded by another male, and young males from two neighboring troops were within ten meters. The resident troop male had fresh lacerations on his face and was huddled with troop females. Ten days later, the two subadult males had returned to the troop and all invasive males were gone.

One of the young males that had been potentially invasive had returned to his natal troop next door, illustrating the manner in which young males may "wait" in their natal troops for breeding opportunities to open-up in the surrounding area (see Chapter 3). Red howler males that remain in their natal troops as subadults and adults and help their father with troop defense are in this respect similar to males that remain as helpers at the nest in many communally nesting birds (see Brown 1987 for a review). By remaining in his natal troop until he attains full adult size and strength, a male should increase his competitive ability outside of the troop after dispersal (Bekoff 1977). When adult male tenure in a troop was shared by father and son, the son eventually became the dominant male in at least two cases, thereby "inheriting" the troop from his father. A relatively old male will eventually lose his ability to win in aggressive encounters with

younger, more robust animals. He may be able to increase his fitness more at this point by helping his son establish and maintain tenure than by trying to gain reproductive status in another troop on his own.

Comparison of duration of association times between related males to those that are not related indicates that, although both types of association occur in the population, those between relatives are more stable and tend to last longer. A dominant male that forms a coalition with a relative can expect to have longer reproductive tenure than in a coalition with a non-relative, therefore producing more offspring and directly enhancing his fitness. Although the subordinate male in a coalition between relatives is fathering very few, if any offspring, there may be very few situations in which leaving would increase his fitness. Any opportunity to invade another troop in which he might breed would probably require forming a coalition with another male in which he may or may not be able to assume dominance. In a coalition with a now unrelated male in which he is once again subordinate, his direct reproductive fitness is the same and his inclusive fitness is now zero, especially if by leaving his relative he exposes him to aggressive replacement by another male. He may be able to form a coalition with another relative that was raised in the troop, but again, this will only be advantageous if he can assume dominance and they are successful in taking over a troop of females.

As population density increases and troop size approaches maximum, forming a coalition with another male should become increasingly advantageous as the modal form of troop composition becomes multi-male. Population density of howlers in the gallery forest study area at

Masaguaral was one third to one half that observed in the woodland between 1981 and 1984, and the mean number of adult males per troop ranged between 1.1 and 1.2 (Crockett and Eisenberg 1987). The modal form of troop composition was single-male for all years (Crockett 1985), while in the woodland it was two-male (see above). Since associations between relatives appear to last longer, it is expected that this will eventually become the modal form of male coalition in stable, maximum density populations. The gallery forest population was growing rapidly through new troop formation and increase in size of existing troops (Crockett and Eisenberg 1987). In a population such as this, in which troops are small to medium size and there is suitable unoccupied habitat available for new troop formation, competition for females should be less severe. Forming a coalition will have little to moderate reproductive advantage over competing as a single male in this situation and should be observed, as in the gallery population, less frequently.

CHAPTER 3  
THE INFLUENCE OF INTRASEXUAL COMPETITION  
ON PATTERNS OF DISPERSAL AND INBREEDING

Introduction

Dispersal forms the central link between the behavioral ecology of a species and the genetic structure of its populations. Leaving the known for the unknown must always entail a certain amount of risk, and conflict of interests can be expected to ensue among offspring, between parents and offspring, and between the sexes, over who leaves and how far they must go. The outcome of these conflicts appears to depend upon a complex web of interactions between the distribution of resources, the manner in which they limit each of these population subsets, and differences between the sexes in the amount of investment in offspring (Greenwood 1980; Moore and Ali 1984; Dobson and Jones 1985, Waser et al. 1986). The pattern of dispersal that results determines the rate and pattern of gene flow within and between populations, and ultimately, their potential for evolutionary change.

In most vertebrate species, one sex is more philopatric than the other (Greenwood 1980). The question of who should leave has been generally described as a trade-off between the sexes involving the comparative costs of dispersal and inbreeding depression (e.g., Bengtsson 1978; Greenwood 1980; Waser et al. 1986). The relative

importance of these two factors in determining sex-bias in dispersal has been a subject of some controversy. Sex-biased dispersal has been proposed as a means of avoiding inbreeding for a variety of species (e.g., Itani 1972; Bischof 1975; Harcourt 1978; Packer 1979; Woolfendon and Fitzpatrick 1986). Voluntary emigration and transfer have been cited as evidence in support of the inbreeding avoidance hypothesis (Harcourt 1978; Pusey and Packer 1987; but see Moore and Ali 1984). Greenwood (1980) noted that while inbreeding avoidance may be a function of sex-biased dispersal, it does not predict the direction of the bias. He proposed that a mating system based on resource defense by males should favor male philopatry, whereas a system based on male mate defense should favor female philopatry. When the benefits of philopatry are the same for each sex, he suggested that conflict between the sexes over which dispersed would be resolved on the basis of dispersal cost. Inherent in this argument was the assumption that one sex or the other must disperse. Moore and Ali (1984) examined available data on inbreeding and dispersal in mammals, and concluded that it was unnecessary to explain observed dispersal patterns as a consequence of inbreeding avoidance. They argued that the major cause of dispersal in mammals was intra-sexual competition among males for mates, and among females for resources. Their conclusions were similar to Greenwoods' in relating resource defense to sex differences in competition, but no imperative for sex-biased dispersal was assumed, and inbreeding avoidance was argued to be an unselected consequence of dispersal.

Models examining the relative costs of inbreeding depression and dispersal indicate that animals should emigrate to avoid the costs of

inbreeding when the costs of dispersal are low, but that the costs of dispersal may often outweigh the costs of inbreeding (Bengtsson 1978; Parker 1983; Waser et al. 1986). In small mammals, the latter appears to frequently be the case (Gaines and McClenaghan 1980). Waser et al. (1986) concluded that if dispersal evolved as a means of inbreeding avoidance in mammals, then females should be the dispersing sex, since they can afford to tolerate less inbreeding depression than males. They noted that the opposite pattern is true of most mammal species.

Inbreeding may not always be costly. Smith (1979) and Dawkins (1979) have described situations in which inbreeding may be favored by certain males in polygynous mating systems, regardless of the costs of dispersal. Limited inbreeding among non-close relatives may benefit individuals by maintaining co-adapted gene complexes specific to local conditions (Shields 1982; Bateson 1983). Shields (1982) presented evidence that most dispersers are philopatric relative to the size of their home range areas, and suggested that selection for "optimal inbreeding" may have contributed to this pattern. Whether a cause or a consequence of dispersal, the level of inbreeding in a population is a manifestation of gene flow, and will be an important determinant of the genetic structure of the population.

This study examines dispersal in the red howler monkey (*Alouatta seniculus*). Red howlers are unusual among primates, and among mammals in general, in that both males and females emigrate from their natal troops (Rudran 1979; Crockett 1984). Wrangham (1980) proposed that in folivorous primates (like howlers) lack of competition over a uniform and abundant resource base should lead to female dispersal. Evidence

suggests, however, that competition among female red howlers may be intense (Sekulic 1982; Crockett 1984; Crockett and Pope 1988). Male dispersal in this species is clearly based on competition over groups of reproductive females (Rudran 1979; Crockett and Sekulic 1984; c.f., Chapter 2), but the nature of female dispersal remains poorly understood. Both sexes may spend considerable time as solitary extratroup animals. New troop formation occurs through the formation of associations among extratroup animals, and colonization of an unoccupied area of suitable habitat (Crockett 1985). The objectives of this study were to: (1) document the rate and pattern of emigration and inter-troop transfer in males and females; (2) examine differences in male and female dispersal differences after emigration, and evaluate their effect on gene flow and inbreeding within and between populations; (3) evaluate the costs and benefits of dispersal by comparing the reproductive success and diet quality of dispersers to non-dispersers; and (4) describe the process of new troop formation and evaluate its implications for the evolution of sociality in this species.

#### Methods

The study site was Hato Masaguaral, a wildlife preserve in the central llanos of Venezuela that has been described in numerous publications (e.g., Rudran 1979; Troth 1979; Crockett 1985). Red howlers were separated into two populations, one occupying an open scrub-woodland habitat on the western portion of the study area, and the other a dense, closed canopy gallery forest associated with the Rio Guarico to the east. These two areas were separated by four kilometers of open savannah at their closest juncture. Long-term censusing of



troops in the woodland population was begun by Eisenberg in 1975, and continued by Rudran from June 1976 through October 1978 (Rudran 1979), by Crockett from March 1979 through February 1981, and in February 1983 (Crockett 1985), and by the author throughout 1981, 1984, and the first seven months of 1985. The gallery population troops were censused by Green in 1975, and by Crockett in October 1978, March 1979 through February 1981, and yearly thereafter through 1984 (Crockett 1985). The number of woodland troops censused grew from 14 in 1975 (Eisenberg, pers. comm.) to 33 in 1985 as additional troops were discovered at the periphery of the study area, or were newly formed within. Gallery troops censused grew from eight in 1975 to 23 in 1984 (Crockett 1985). Changes over the ten year study period in population density, troop size, and troop composition are summarized by Crockett and Eisenberg (1987) for both habitats.

#### Rates of Gene Flow and Inbreeding

In 1978 (Thorington et al. 1979) and 1981, 164 animals were captured (see Chapter 2) and marked with unique patterns of colored ear tags that insured positive identification of individuals after dispersal. Both rabbit tags and Monell tags covered with colored, heat-shrink electrical tubing were used. The captured sample included 39 adult males, 36 adult females, 48 immature males, and 41 immature females, collectively representing 14 woodland troops and 4 gallery forest troops. Additional animals were individually recognizable by characteristics such as skin depigmentation patterns, missing digits, permanent scars, and torn ears and lips. In the 1981 captured sample, 61% of combined adult and subadult males, and 50% of combined adult and

subadult females exhibited injuries of the type used in individual identification (Crockett and Pope 1988).

Two types of gene flow were distinguished: (1) that which occurred among troops within a population; and (2) that which occurred between populations. Gene flow among troops within a population was measured in the woodland habitat through relocation of individuals, recognizable either by eartags or other characteristics, that had emigrated from the troops in which they were first located in 1981. Dispersal events that occurred during the five years previous to this time that are reported by Rudran (1979), Thorington et al. (1979), Sekulic (1981, 1983), and Crockett and Sekulic (1984) were also included. Only troop immigrants, either those individuals that successfully entered established troops, or that formed new troops, were considered to contribute to effective gene flow within the population. In all immigration events, the identity of the immigrant (either known or unknown) was established, and the distance travelled from the last troop that they were known to occupy was recorded in terms of the number of troop home range diameters that were traversed. Mean home range diameter was estimated to be 274 m in the woodland habitat, based on home range areas reported by Crockett and Eisenberg (1987), and Sekulic (1982). Unknown individuals were either animals that came from outside of the population, or unmarked animals that had emigrated from troops within the study area and were unrecognizable. Immigration events involving unknown males were classified with regard to whether they occurred in troops at the periphery or center of the study area, and as to whether they occurred

before or after the 1981 marking period. The relative percentage of unknowns in these combined categories were calculated.

Inbreeding, which is equivalent to zero gene flow, was characterized in terms of male dispersal distance, since breeding females were always recruited from within their natal troop once it had been established (Crockett 1984). A male that remained in his natal troop after reaching sexual maturity, or that maintained tenure long enough to breed with his daughter, was considered to have travelled zero dispersal distance. Dispersal distance was thus calculated on a per generation basis, which was estimated to be the time from the birth of a female to the birth of her first daughter, or five years (Crockett and Rudran 1987b).

Rate of gene flow between the woodland and gallery forest populations was estimated from the percent of marked dispersers sighted that had relocated from one population to the other. Rate of gene flow among troops within the woodland population was considered to be equivalent to male tenure length, since females were almost never able to immigrate into established troops (Crockett 1984; see also below). Successful new troop formation, in which all individuals were "immigrants", was a relatively rare event in the woodland population, and is treated as a special case below. A new male tenure was assumed to begin at male replacement following the successful invasion of a troop by outside males, and when a status change occurred between two males that co-inhabited a troop. Since paternity exclusion using genetic markers indicates that only one male in a multi-male troop does all or most of the breeding (see Chapter 2), only one male at a time was

assumed to be contributing to any single troop gene pool. An immigration event involving two or more males was therefore considered equivalent to a single migrant. Although a status change between the immigrant males may occur at some later time, this was considered equivalent to a new immigration event corresponding to the beginning of a new male tenure. Since many male tenures were indeterminate (i.e., either ongoing at first or last troop contact) mean male tenure length was calculated using a clinical life table analysis of survivorship in which tenures could enter the study at any time and be withdrawn prior to their termination (Peto et al. 1976). Mean life expectancy of a tenure was calculated as  $e(x)$ .

Additional information on dispersal distance was obtained by monitoring the movement patterns of radio-collared migrants. Three solitary females and four solitary males were captured in the manner described in Chapter 2, and fitted with radio collars. Collars wrapped snugly above the hyoid apparatus and below the base of the skull allowed full expansion of the pharyngeal cavity and did not audibly interfere with howling ability. One of the radio-collared males was able to successfully evict a male from an extra-troop association of estrous females after two days of aggressive display that included extensive bouts of howling. Thus the collars did not appear to impair competitive ability. Animals were recaptured prior to radio battery expiration, and the collars removed.

The troop of natal origin was known for three of the males and one of the females. Each animal was located at least twice per week for a minimum of two months. All animals were located during the middle of

the same day as often as possible, such that time between most consecutive location dates was the same for each sample. Once every month, each animal was located for five consecutive days, and mean distance travelled per day was determined. The total area occupied by an animal was calculated using a minimum convex polygon algorithm (Eddy 1977). Cumulative area covered after each month of observation was calculated for both sexes, and the means were compared.

Patterns of use within ranging areas were examined through harmonic mean transformation of location data points and the development of contour lines containing 20%, 40%, 60%, 80%, 90%, and 100% of the total array of location sequences. The Shannon-Weiner information index was used to measure differences among individuals in quadrat utilization diversity within ranging areas. Each minimum convex polygon was divided into 200m quadrats, and the percentage of total location points per quadrat determined. The diversity index

$$H = - \sum p_i \ln(p_i)$$

was calculated for each polygon, where  $p_i$  is equal to the proportion of total locations in the  $i^{\text{th}}$  quadrat (Struhsaker 1975; Wilson and Bossert 1971). Since sample size varied according to the total number of quadrats per range area, ranging diversity was expressed as the percentage of the maximum H possible for the number of quadrats used. Maximum H was found by dividing location points equally among all quadrats within a polygon, and calculating the diversity index that would result from this distribution.

## Costs and Determinants of Dispersal

The development of matriline within troops is an important factor in determining patterns of genetic differentiation within populations (see Chapter 4). The genetic relationship between those females that bred in their natal troop and those that dispersed was determined with regard to maternal lineage. Number of adult breeding females already in the troop at the time of dispersal was calculated for each dispersal event, and the percentage of natal females that dispersed was compared in troops containing one, two, three, and four adult females. The degree of relatedness among females in newly formed troops (see below) was compared to that among females in the 16 established troops in which natal females had remained to breed.

Paired activity budget samples were collected for ten extra-troop males and nine extra-troop females in the woodland habitat. An extra-troop animal was observed for twelve hours per day on a minimum of three consecutive days. An identical sample was immediately collected on a troop animal of the same age and sex class that occupied a home range that overlapped as much as possible of the area used by the extra-troop individual. Group females used in the comparisons were neither pregnant nor lactating. All food items eaten during the last eight paired activity budget samples (three female pairs and five male pairs) were marked, and collected immediately afterwards in quantities sufficient to yield a minimum of ten grams dry weight material. The low stature of the woodland canopy allowed food samples to be collected from the exact location on the tree or shrub at which the food item was being selected approximately 90% of the time. If the exact location could not

be reached, the sample was collected from another location on the same tree, or a tree of the same species nearby. Samples were dried at between 45 and 50 degrees centigrade, and stored in a dry-box until laboratory analysis.

Standard nutritive component analysis techniques were used to determine the percent ash-free neutral detergent fiber (Goering and Van Soest 1970, Golding et al. 1985), percent concentration of total (Kjeldahl) nitrogen and phosphorus (Gallaher et al. 1975, Hambleton 1977), and in vitro digestibility (Goering and Van Soest 1970) of each food sample. Solitary and group diets were compared within each sex in terms of the percent representation of each nutrient within the total array of food items selected. Means were compared using t-tests and analysis of variance on arcsin transformed data. Age of first reproduction of females that dispersed was compared to that of females that emigrated. These data, in conjunction with previously published information on rates of injury for solitary and group animals (Crockett and Pope 1988), were used to examine costs of dispersal for both sexes.

#### New Troop Formation

Associations of extra-troop animals were designated as troops when they produced offspring. New troop formation observed in the woodland population between 1981 and 1985, in addition to those data reported by Crockett (1985), were used to calculate rate of new troop formation and percent failure. Infant mortality rate in new troops was compared to mean infant mortality for all troops.

The development of associations among extra-troop animals was the precursor to new troop formation. During both the paired activity

budget samples, and visual locations of the radio-collared animals, other howlers that these individuals were associating with were described. During the activity budget samples, length of time spent with each associate was recorded. Migration distances and genetic relationships among new troop males and females are compared to those for established troops, and used to assess the effects of new troop formation on gene flow within and between populations.

### Results

#### Gene Flow and Inbreeding

Females. Between January 1981 and July 1985, 62 juvenile females (i.e., classified as juveniles at the onset of observations or born during this period) reached sexual maturity. Forty-five of these (73%) disappeared from their natal troop at an age when dispersal typically occurs (2 - 4 years; Crockett 1984), while 17 (27%) remained in their natal troop (Table 4). Fifteen of the 17 that remained had borne infants by the end of the study period. Two additional marked females dispersed when their natal troop dissolved, but it could not be ascertained whether they would have stayed or emigrated if the troop had remained intact. No instance of a female dispersing from a troop in which she had reproduced was observed except in those cases in which the entire troop failed and dissolved (see below). Crockett (1984) reported a female natal dispersal rate of 33.3% for the woodland and gallery study areas combined between October 1978 and February 1981. This proportion, however, included all juvenile females regardless of whether they had reached sexual maturity, such that many of those that had not emigrated may still have done so before breeding. She also observed a



Table 4. Summary of male and female gene flow among troops within the woodland population.

	Females	Males
Natal Dispersal:		
Stayed as Adults	27%	6%
Left	73%	94%
Percent of Identifiable Dispersers that Joined Troops Within Study Population	10%	67%
Mean Primary Dispersal Distance: Place of birth to place of first reproduction	6 hrd*	1 hrd
Mean Secondary Dispersal Distance	none	1 hrd
Immigration Rate Into Established Troops	none	0.67 male per generation

\* hrd = home range diameter.

complete absence of emigration among females once they had attained breeding status within troops, as did Rudran (1979) during his 1976-1978 census period.

Twenty of the females that dispersed were unmistakably recognizable through ear tags or unique physical characteristics. Only two (10%) of these stayed in the woodland study area and bred, both as members of newly formed troops (Table 4). The remainder disappeared from the study population before reproducing. One tagged disperser was found dead, and another was relocated in the gallery forest population six km away from her natal troop (see below), but the fates of the rest were unknown. No female, marked or unmarked, was observed to successfully immigrate into an established troop (i.e., any association of animals that had already produced offspring). Crockett (1984) observed female immigration into established troops twice between October 1978 and February 1981, but one of these involved a female that rejoined her natal troop after having emigrated from it several months earlier. Rudran (1979) observed only one case of female immigration between June 1976 and April 1978, but the female remained peripheral and had suffered over twice the infant mortality rate of the other two females in the troop by mid-1985. Thus over a nine year period only two cases of female migration between troops were observed.

Although migrant females frequently attempted to approach troops, they invariably met with aggressive resistance from troop females. All nine of the solitary females from the activity budget samples were chased by troop females at least once during the sample period. Additional cases of troop females behaving aggressively towards outside

females were observed during censusing, troop activity budgets, and during two activity budgets on solitary females that were aborted when the female could not be relocated after being chased by troop females. Such chases were twice observed to result in the retreating female being caught and bitten. Solitary females had the highest injury rate of any sex-status class in the population (solitary males, troop males, and troop females), and were the only group in which the majority of injuries were concentrated at the posterior end of the body (Crockett and Pope 1988). The female observed to immigrate into a troop during Rudran's (1979) study followed the troop for four months, during which time she was repeatedly chased and bitten by the troop females. Sekulic (1982) observed a solitary female trail a troop in a similar manner for over 11 months. During 10 full day observation periods, troop females chased or displaced her 34 times and howled at her for a total of 152 minutes. She was not successful at attaining even peripheral troop membership.

Distance from place of birth to place of first reproduction was observed for only three females that dispersed from their natal troop (Table 4). Female 5241 became a member of newly formed troop M82, six home range diameters (1.65 km) from her natal troop. Female 7161 became a member of newly formed troop M96, six home range diameters (1.6 km) from her natal troop. Female 6662, who dispersed prior to 1981, became a member of newly formed troop M70, 3.5 home range diameters (0.96 km) from her natal troop. All three females had given birth to at least one infant by the end of the 1985 study period.

Four additional females that dispersed were subsequently located as either solitaires or members of extra-troop associations. Female 5782 was located in the gallery forest study area as a member of a bisexual association approximately six km from her natal troop. Female 7583 was seen as a solitary approximately two home range diameters (0.55 km) from her natal troop (Crockett, pers. comm.), but subsequently disappeared from the woodland study population. Female 6284 was observed as a member of an extra-troop association that formed in the area that her natal troop had occupied before it dissolved (Crockett, pers. comm.). She was sighted as a solitary in the same area in 1984, one year later, but the association no longer existed. She also disappeared from the study population. Female 7982.1 died four home range diameters (1.1 km) from her natal troop (see below).

The minimum convex polygon areas covered by each of the three migrant females that were radio collared are illustrated in Figure 2. Mean area covered was  $1.33 \text{ km}^2$  (133 ha) over a mean observation time of 3.8 months. This was approximately 24 times larger than the mean troop home range size in the woodland habitat of between 4 and 7 ha (Crockett and Eisenberg 1987). Mean distance travelled per day was 316 m. Mean cumulative area increased steadily from 35 ha after one month of observation to 160.5 ha after four months of observation (Figure 7). All three females exhibited a range use pattern in which the area contained within the 90 percentile contours was roughly half the size of the total area (Figure 3, Table 5). Mean quadrat utilization diversity was 2.75. Diversity indexes were, on average, 79% of  $H_{\max}$  (Table 5).

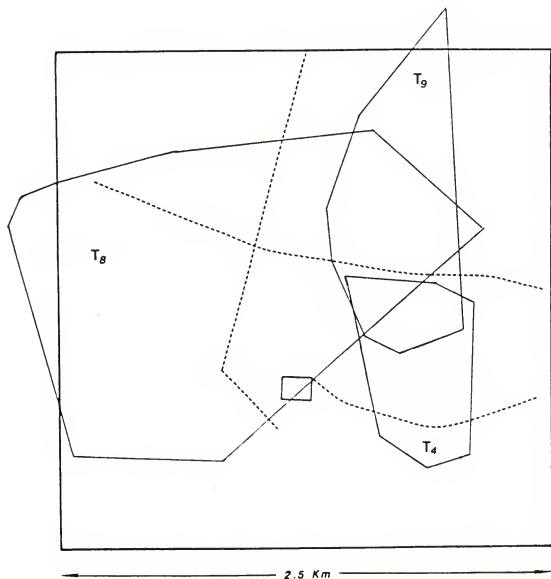


Figure 2. Total ranging areas of radio-collared, migrant females: minimum convex polygons.



Figure 3. Harmonic mean contour plots for ranging areas of three migrant females. Areas enclosed within contours are listed in Table 6.

Table 5. Comparison of ranging patterns of radio-collared male and female solitary migrants.

	Solitary Females	Solitary Males
Mean Observation Period	3.8 months	3.75 months
Mean Ranging Area: Minimum Convex Polygon	133 ha	42 ha
Mean Displacement Distance Per Day	316 m	208 m
Mean Quadrat Utilization Diversity (H)	2.75	2.04
Percent of Maximum Quadrat Utilization Diversity ( $\%H_{\max}$ )	79%	75%

T4. Female T4 (Figure 3) had one major use area in the northern part of her range, and a minor use area in the southern part of her range that was immediately adjacent to her natal troop home range. Quadrat utilization diversity was 82% of  $H_{\max}$  while mean distance travelled per day was 159 m. She had emigrated from her natal troop M79 by November of 1984, and was located as a solitary approximately three home range diameters away in January 1985, at which time she was radio-collared. She died 4.5 months later, possibly of a pathogen. Her body was found intact on the ground, lying apparently in the position in which it had fallen. She had been observed on the last visual contact prior to her death with green mucous draining from her nose, a condition that had been observed occasionally in other animals in the population (e.g., see Crockett and Pope 1988).

T8. Female T8 (Figure 3) had three major use areas distributed throughout her range. Quadrat utilization diversity was 80% of  $H_{\max}$  while mean distance travelled per day was 464 m. She travelled extensively between these areas, occupying at least two of them, and usually all three, during each of the four months that she was observed. During the month of April, for example, she travelled a total of 8.2 km between consecutive location points, whereas female T4 travelled only 1.6 km over the same location dates. She made numerous forays outside of these areas, particularly to the northeast. After four months of observation, her collar was found at the bottom of a lagoon in an open scrub area that was 500 m from the nearest tree. She was last located visually one week prior to this time in a group of trees surrounded by the water from a connecting lagoon, and appeared to be in good health.



Although no body could be found, the location of the collar suggests that she may have been a victim of predation, possibly by one of the numerous spectacled caiman (*Caiman crocodilus*) that occupied the lagoons. Both troop and solitary howlers were observed to cross over open ground inundated with water in traversing their ranges during the activity budget samples. Caiman measuring two meters or more had been captured in the study area (John Thornbjarnerson, pers. comm.), and during the previous year had attacked three domestic animals as large or larger than an adult howler.

T9. Female T9 (Figure 3) had one large major use area in the northern part of her range, but made numerous forays to the south. Quadrat utilization diversity was 76% of  $H_{\max}$  while mean distance travelled per day was 326 m. During the last month that she was monitored she became a member of an extra-troop association that attempted to defend a territory within her core use area, where she then spent the remainder of her time. Her collar was removed after 2.75 months of observation. She weighed the same as at the time of her initial capture, and appeared to be in good physical condition.

Males. Between January 1981 and July 1985, 63 males born in the woodland population reached sexual maturity. A male was considered to be an adult when he attained full weight at approximately six years of age (see Chapter 2). The earliest age of reproduction for a male of known age in the population was also six years. Fifty-nine (94%) of these individuals disappeared from their natal troops at an age when dispersal typically occurs (3 - 7 years, Crockett 1984). Seven of these emigration events were the result of troop take-overs by outside males.

Only four males originally classified as juveniles in January 1981 (6%) remained in their natal troops after reaching six years of age (Table 4). Six additional males that had reached sexual maturity before 1981 remained in their natal troops well into the 1981 - 1985 study period. Two of these males (aged 9 and 10 yr) were evicted along with their presumed fathers after troop take-overs, two had become the breeding males in their respective natal troops, and two finally emigrated (aged 8.5 and 11 yr).

Out of a total of 70 troop immigration events within the woodland study area, 47 (67%) were known males from within the population. The proportion of immigration-aged males in the population that were individually recognizable from ear tags and unique physical characteristics was approximately 75 percent (50 percent of all males that were this age or older between 1981 and 1985 were ear-tagged, and 50 to 60 percent of the remainder had injuries of the type used in individual recognition; see Crockett and Pope 1988). Thus the percentage of known troop immigrants corresponded well to the proportion of males in the population that could be identified after dispersal. Seventeen of the 23 immigration events that involved unknown males (24% of total immigrations) either occurred before tagging in 1981, or in troops on the periphery of the study area that were more likely to be invaded by males from outside of the study population.

Distances travelled per generation by known immigrant males from their troop of origin are summarized in Figure 4. The 19 "non-immigration" events, in which a male remained in a troop long

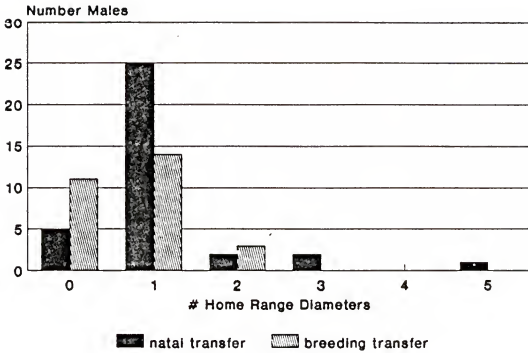


Figure 4. Distances travelled per generation by known immigrant males from their troop of origin. Mean home range diameter is 275 meters.

enough to potentially breed with his mother or daughter, were classified as dispersal distances of zero. Mean dispersal distance of males leaving their natal troops was one home range diameter. Mean dispersal distance of males from troops into which they had previously immigrated was somewhat lower (0.7 home range diameters) due to the large number of males that held reproductive tenure for longer than five years (zero dispersal distance). Mean dispersal distance for all males combined was one home range diameter. Immigration rate, expressed as mean survivorship of male breeding tenure, was one male every 7.6 years. Based on a female generation time of five years, this was equivalent to one male every 1.5 generations.

The areas covered by the four radio-collared, migrant males are represented in Figure 5. Mean minimum convex polygon area of the four ranges was  $0.42 \text{ km}^2$  (42 ha) over a mean observation period of 3.75 mo. Mean distance travelled per day was 208 m, which was significantly less than the 316 m per day travelled by females ( $p < .05$ ,  $F = 5.32$ ,  $df = 1$ ). Mean cumulative area covered per month increased from 6.9 ha after one month of observation to 68.3 ha after five months of observation, and was consistently lower than that of females for all monthly increments (Figure 7). Patterns of use within these areas are illustrated in the harmonic mean contour plots for each male (Figure 6, Table 6). The 90% contour contained nearly 60% of the total area covered by males T2 and T10, 45% of the area covered by male T5, and only 16% of the area covered by male T6. Mean index of quadrat utilization diversity was 2.04. Diversity indexes were, on average, 75% of  $H_{\max}$  (Table 5).

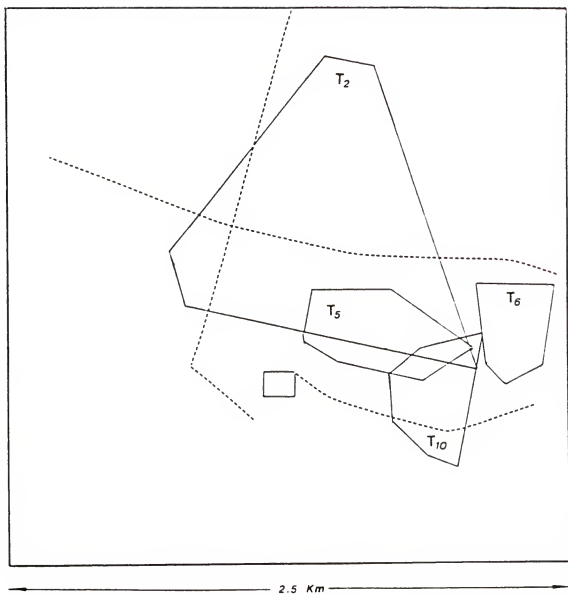


Figure 5. Total ranging areas of radio-collared, migrant males: minimum convex polygons.

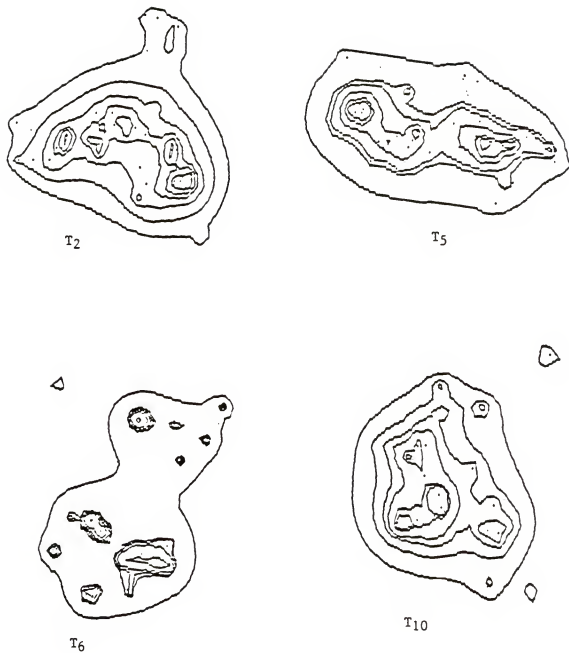


Figure 6. Harmonic mean contour plots for ranging areas of four migrant males. Areas enclosed within contours are listed in Table 6.

Table 6. Areas contained within harmonic mean contour percentages for radio collared males and females.

### FEMALES

Animal	Area Contained Within Contour Percentages (km <sup>2</sup> )					
	20%	40%	60%	80%	90%	100%
T4	0.012	0.030	0.077	0.138	0.252	0.419
T8	0.109	0.280	0.608	1.324	2.133	3.827
T9	0.025	0.042	0.1842	0.403	0.633	1.299

### MALES

Animal	Area Contained Within Contour Percentages (km <sup>2</sup> )					
	20%	40%	60%	80%	90%	100%
T2	0.013	0.068	0.208	0.487	0.840	1.434
T5	0.004	0.013	0.042	0.103	0.138	0.312
T6	0.000	0.000	0.011	0.017	0.022	0.133
T10	0.004	0.011	0.036	0.065	0.107	0.187

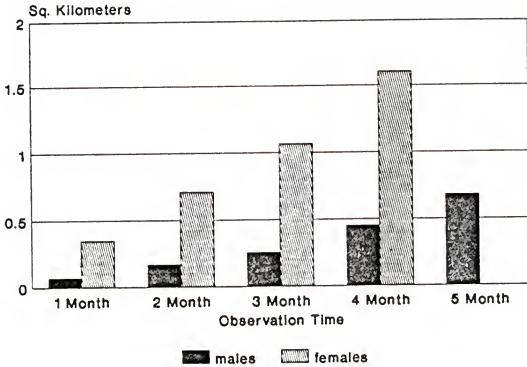


Figure 7. Mean cumulative ranging-area increase as a function of observation time for solitary, radio-collared males and females.



T2. Male T2 covered the largest area of any of the four males (Figure 5). Cumulative area covered was two to three times larger than those of the other three males from months two through four. During the fifth month of observation his range shifted abruptly to the north, where he began interacting with the association containing female T9. His cumulative ranging area then increased from 69.5 ha to 115.6 ha, and was five times larger than that of the only other male that was observed for five months (T5). His core use area was spread throughout the central part of his total range prior to month five (Figure 6). Quadrat utilization diversity was 76% of  $H_{\max}$  and mean distance travelled per day was 244 m.

T5. Male T5 emigrated from his natal troop M63 by September of 1984. He was found as a solitary approximately 200 m south of his natal range in January 1985, at which time he was radio-collared. Cumulative area covered by male T5 increased by only 15% from months three to four, and remained the same from months four through five. Quadrat utilization diversity was 75% of  $H_{\max}$  and mean distance travelled per day was 182 m. He shifted gradually from the core use area on the western side of his range to that on the eastern side (Figure 6), spending the majority of February and March in the western area, May and June in the eastern area, and splitting April between the two. His total ranging area of 21 ha was three times larger than his natal home range, which he overlapped completely. Although he was observed visually in 46 out of 62 location data points, and followed continuously for four days, he was never observed within the same part of his natal range as the troop, and did not interact with them. He successfully took over an extra-troop

association of two estrous females at the beginning of month five, and they collectively defended an area immediately adjacent to his natal home range until the end of the observation period.

T6. Male T6 emigrated from his natal troop M78 by September 1984. He formed an association with the recently evicted male from the neighboring troop along with another subadult male, and they successfully re-invaded the evicted male's troop (M77). In January 1985, male T5 was found approximately 300 m away from troop M77. Both he and the adult male had fresh wounds on their faces, and a three month old infant had disappeared. Male T5 was radio-collared at this time. He never rejoined troop M77, but continued to range on his own within the same area. His cumulative ranging area over the 1.75 months that he was observed (13.7 ha) overlapped both his natal home range and that of troop M77, and was similar in size to those areas covered by males T5 and T10 after two months (13.9 ha and 16.2 ha, respectively). The largest concentration of locations was in the southeast of his range in an area that was not being used by any troop (Figure 6). Quadrat utilization diversity was 80% of  $H_{\max}$  and mean distance travelled per day was 198 m. After seven weeks of observation, his collar was found on the ground beneath a tree. The entire ranging area was searched extensively for three days, but no sign of male T6 was found. It was assumed that he was either a victim of predation, or had managed to slip his collar off. The latter seemed more likely, since there were no caiman in the area due to the dry season, and it is improbable that the other possible predators in the woodland habitat would be large enough to take a full-grown howler male (see Crockett and Pope 1988), and

remove a collar without leaving any sign of remains in the area. Males were more difficult to fit with collars than females due to the lack of a distinct neck region, and the size of the hyoid apparatus. Three previous collaring attempts on other males had ended in the male being able to remove the collar, but always before the end of one month.

T10. Male T10 emigrated from his natal troop M73 by March 1985. He was found as a solitary within his natal home range in early April, at which time he was radio-collared and then followed for three months. Cumulative area covered after three months of observation (17.3 ha) was nearly identical to that observed for male T5 after three months (17.6 ha), and about one third that of male T2 (66.6 ha). Total ranging area was three times larger than his natal home range, and overlapped with approximately 75% of it. He was observed visually in 28 out of 33 location data points, but was never seen interacting with his natal troop. Almost all of the area contained within the 80% contour line (Figure 6) was used each month. Mean distance travelled per day was 208 m, and quadrat utilization diversity was 75%  $H_{max}$ .

Inbreeding. Direct inbreeding could occur when a male becomes the breeding male in his natal troop, and when a male is able to hold breeding tenure long enough to breed with a daughter that does not disperse. Only during the last three years of observation were animals of known parentage in the population generally old enough to detect such events. The former appears to have occurred at least twice (troops M62 and M54; see Chapter 2), although in the case of troop M54 no infants were produced between the time of the natal male's ascension to dominance in 1984 and the end of the study period in 1985. Both females

in the troop were also natal, and may have been the breeding males' sisters or half sisters. The breeding male in M62 produced at least three offspring by the time the troop dissolved in 1982 (see below), one of which was by his probable mother. In 1984 and 1985, natal females in troops M79 and M61 gave birth to infants while their fathers were still the breeding males in their respective troops. In other cases wherein females gave birth in their natal troops, either male tenure change had occurred, or it could not be ascertained whether the breeding male was the natal female's father (i.e., she was already born when first troop census contact was made).

Between populations. During the 27 month period from December 1981 through February 1984, 37 marked individuals emigrated from the woodland troops that they were living in at the time of marking. Two of these animals were sighted during this period in the gallery forest as members of extra-troop associations (Crockett 1985). Assuming that the proportion of marked individuals sighted in the gallery is equivalent to the proportion of all woodland dispersers that immigrate into the gallery, then out of the 100 animals that actually emigrated during this period, between five and six should have migrated to the gallery. The total number of woodland immigrants to the gallery per generation (66 months) was thus estimated to be between 12 and 15 animals. Gallery dispersers that enter the woodland population will probably be lower due to lower population density in the gallery forest, and not all migrants will breed, so realized effective migration rate (Wright's  $N_{gm}$ , 1969) between the two populations will be somewhat lower.

## Costs and Determinants of Dispersal

Determinants. By the end of the 1985 study period, 16 of the 33 troops being censused in the woodland study population had recruited natal troop females as breeders. The relationships between these females and those already in the troop at the time they were recruited are described in Table 7. In the eleven cases in which only one natal female had been recruited, four consisted of mother-daughter pairs, and four of a mother and daughter plus an additional female of unknown relationship. In one of these the unknown female was possibly a half-sib of the mother, since both were nulliparous adult females when the troop was first contacted. The remaining three were cases in which the natal female was already a juvenile when the troop was first contacted, and an older adult female that was in the troop at that time had died. Thus it could not be determined which of the other females in the troop, if any, was the natal female's mother. In six cases, two or more natal females were recruited:

2 females recruited. Troop M63 consisted of two natal females and a third female of unknown origin, but the relationship among them could not be determined. Both of the breeding females in troop M54 were natal, and were either sibs or half-sibs. Troop M79 consisted of two adult females of unknown relationship, and two of their daughters. One of the natal females' mothers was known, but which of the original two females had mothered the second was not known. Troops M67 and M73 both consisted of two females of unknown relationship and two daughters of one of the females.

4 females recruited. Troop M75 consisted of two adult females that were sibs or half-sibs, and two of the daughters of one of those females. All four were born in M75.

In all three cases in which the identity of the mother of more than one natal recruit in a troop was known, both were the daughters of a single female. In troop M75 three, and possibly all four of the breeding females in the troop were the descendants of a single female. Aggression directed by females towards the daughters of other troop females as they approach reproductive age has been described extensively by Crockett (1984), and was observed by the author in troops M61 and M67. In troop M62, fights between the two adult females in the troop that resulted in severe injury to both parties immediately preceded the disappearance of both of one of the females' (6222's) daughters (Crockett 1984). The other adult female (6221) had recently given birth to a new infant on both occasions. Three months after the death of female 6221 in January 1981, one of 6222's daughters that had dispersed rejoined the troop. Competition among troop females may thus strongly influence who's daughters remain as breeders in the troop, such that only those of the dominant female are likely to be successful. As natal females replace founder females as troop breeders, patterns of relatedness should tend towards single matriline. In addition to the three four-female troops in which this was demonstrated, four of the five two-female troops were mother-daughter pairs, and the fifth (M54) was possibly full sibs.

In new troops, wherein the breeding females are derived from extra-troop animals that have formed associations, females may be

completely unrelated to each other. In the four cases in which the identity of a female that joined a new troop was known, she could not have been related to the other female(s) in the troop. Although it is possible that females of dispersal age may be able to leave their natal troop together, two females disappearing from the same natal troop at about the same time (within a two month interval) was observed only once in the 45 female dispersal events that took place during the study period.

The percentage of natal females that dispersed on or before reaching maturity increased as the number of breeding females already in the troop increased (Figure 8). In single female troops, usually resulting from the death of one of the adult females, none of the natal females that reached reproductive age dispersed. Fifty-five percent of maturing females dispersed from troops with two adult females, 90% from troops with three adult females, and 100% from troops with four adult females.

Costs. The diet qualities of group females, group males, solitary females, and solitary males are compared in Table 8. Those food items eaten by group females were significantly higher in both crude protein ( $p < .001$ ) and phosphorus ( $p < .001$ ) than those eaten by solitary females, solitary males, or group males. In vitro digestibility was also somewhat higher in group female diets, but variance within groups was high and none of the group means differed significantly from each other. The percent ash-free neutral detergent fiber (NDFA) in group female diets was significantly lower than that found in the other three groups ( $p < .05$ ), especially solitary and group males. The NDFA content of

Table 7. The influence of natal female recruitment on the genetic relationship among troop adult females.

	No. Natal Females/Troop that Remained and Bred		
	1 Recruit (9 troops)	2 Recruits (5 troops)	3 Recruits (2 troops)
Number of Mothers	1: 9	1: 2	1: 1(p.)
per Troop that	2: 0	2: ?	2: ?
Recruited Daughters	unk: 0	unk: 3	unk: 1
Number of Troops Comprised of a Single Matriline	3	?	1
Number of Troops Comprised of a Single Matriline plus One Female of Unknown Relationship (i.e., she may or may not be related)	3	2	1



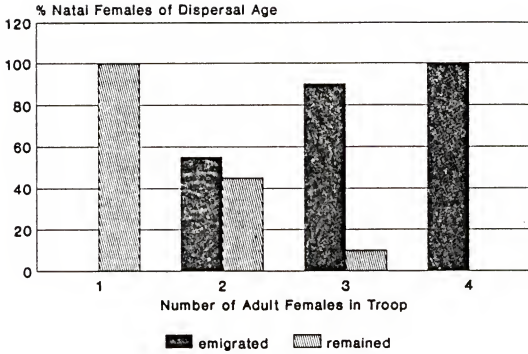


Figure 8. Natal female emigration as a function of the number of adult females in the troop.

Table 8. Comparison of nutrient component analysis of diets eaten by solitary and group-living males and females. IVOMD = in vitro digestibility; NDFaf = ash free neutral detergent fiber; P = phosphorus. Numbers in parentheses beneath values are standard deviations, and values followed by asterisks are statistically different from other means for that nutrient. \*  $p < .05$ ; \*\*\*  $p < .001$

	% Crude Protein	% IVOMD	% NDFaf	% P
Group Females	20.4 *** (9.2)	50.4 (18.0)	43.4 * (9.3)	0.288 *** (0.140)
Solitary Females	13.5 (6.9)	44.5 (14.1)	47.0 (10.1)	0.187 (0.082)
Group Males	13.6 (7.1)	45.1 (14.5)	50.7 (10.0)	0.213 (0.105)
Solitary Males	14.1 (7.3)	46.9 (17.3)	50.5 (10.3)	0.191 (0.110)

solitary female diets was also lower than that found for solitary and group males ( $p < .06$ ). Group male and solitary male diets did not differ significantly in any of the four nutrient categories.

Mean age of first reproduction for the three females that dispersed from their natal troops and became members of newly formed troops was seven years. This was significantly different from mean age of first reproduction of 5.5 years for females that reproduced within their natal troops (Mann Whitney U statistic,  $p < .05$ ).

#### New Troop Formation

Extratroop associations. An extratroop association was defined as any group of two or more howlers in which no infants had been born. Total activity budget observation time for each of the two sexes was divided into percent of days spent alone, percent spent with individuals of the opposite sex only, percent spent with individuals of the same sex only, and percent spent with mixed-sex groups of individuals (Figure 9). In both sexes, animals were alone during slightly more than half of total observation time. Although almost no time was spent by either males or females with individuals of only the same sex on a continuous basis, mixed-sex groups separated and came together again on an hourly basis during almost any given observation day. Splinter groups of this sort were frequently composed of pairs of females, but rarely pairs of males only. In fact, all four of the mixed-sex associations in which the sample animals participated revolved around stable female duets. Although the female pair was never alone for the duration of an entire sample, the other animals associating with them were subject to change.

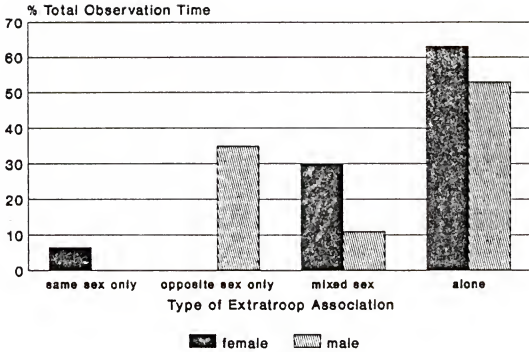


Figure 9. Percent total observation time spent by extratroup animals during activity budget samples in different types of associations.

Individual females spent no continuous time with individuals of the opposite sex only, whereas males were in associations of this type during 35% of the total time during which they were observed (Figure 9). While associations typically contained only one male and two females, several males with one female was not observed. Male-female pairs were never observed to last longer than one day, and were usually parts of larger groups. The majority of continuous female association time (30% of total time) was spent with individuals of both sexes, whereas the majority of association time for males (35% of total time) was spent with individuals of only the opposite sex.

While activity-budget animals were never observed to participate in more than one association during the three to four day sample period, visual location data taken on radio-telemetry animals over a period of several months illustrates the frequency with which extra-troop individuals interact with other migrants within their ranging area (Figure 10). Associations were considered to differ if they did not share at least 50% of their members. Males were found associating with other howlers in 21% of 87 visual location samples. Mean number of different animals that each male associated with was five, representing 2.75 different associations. Females were sighted with other animals in 33% of 61 visual locations. Females associated, on average, with six different animals apiece over the course of the observation period, representing 3.67 different associations.

New troop formation. New troop formation in the woodland habitat is summarized in Table 9 for the years 1981, 1982 through 1983 (from

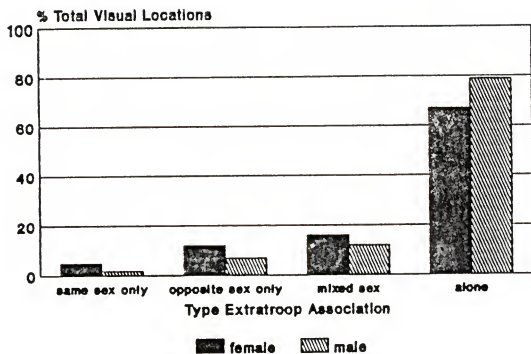


Figure 10. Percent total visual locations in which extratroup animals were observed in different types of associations during radio-telemetry monitoring.

Table 9. Reproductive correlates of new troop formation. A new troop "cohort" is defined as the new troops formed during a particular time period. Asterisks indicate contribution of data from Crockett, 1985.

	(1979)/81 *	1982/83	1984	1985
Number of New Troops Formed	2 *	5 *	5	2
Number of New Troops with Offspring > 1 year	2	2	2	0
Number of New Troops with Offspring of Dispersal Age	1 .	0	0	0
Mean Interbirth Interval Within New Troop Cohort	23.2 mo.	25.8 mo.	---	---
Percent of Infant Survival Within New Troop Cohort	67 %	60 %	50 %	---
% Failure of New Troop Cohort	0.5	0 .4	0.4	0

Crockett 1985, Table 1), 1984, and the first half of 1985. Rate of new troop formation increased between 1981 and 1984, possibly due to the failure and dissolution of two established troops that left two territories open for colonization (Crockett 1985). Troop failure rate was 40% - 50% for all time intervals except 1985, in which year the two new troops had only recently born their first infants. Mean survival rate of infants to one year of age was 56%, which was over one third lower than the population mean of 80% reported by Crockett and Rudran (1987). Only six of the 14 troops had produced infants that survived one year, and only one troop had produced offspring that reached dispersal age (2.5 yrs for females and 3.5 yrs for males; Crockett 1984). Interbirth intervals could be calculated only for 1981 and 1982-83, since none of the females in the troops that formed after that time had given birth to more than one infant. Mean interbirth interval of 24.5 months was 30% longer than the population mean of 17 months (Crockett and Rudran 1987).

Female immigration into new troops that had produced offspring surviving to one year contributed only 0.24 females per generation to the overall among-troop migration rate within the population, or about one female every 20 years. If the two females that were successful at immigrating into established troops are included, total female immigration rate was 0.27 females per generation. Male immigration rate into new troops, including tenure changes since the birth of the first infant, was incorporated into the overall analysis of male migration rate. While 24 % of all female dispersers in the woodland population were either marked or otherwise identifiable, only 9% of the females



that immigrated into new troops could be identified. Mean migration distance was six home range diameters (see above). Seventy one percent of all breeding males that immigrated into new troops could be identified. Mean dispersal distance for these males was one home range diameter.

### Discussion

#### Costs and Determinants

Both male and female red howlers emigrate from their natal troops, but only males are able to transfer after dispersal into other established troops. Females must find unoccupied territory in which to form a new troop with other migrants. While both sexes are philopatric when possible (i.e., females remaining in their natal troops and males transferring to neighboring troops), those females that emigrate travel at least six times farther than migrant males before breeding. This pattern is the opposite of that typically observed in mammals, in which males disperse farther than females (Greenwood 1980). Greenwood (1980) has suggested that when familiarity with an area is advantageous to reproduction for both sexes, conflict between the sexes may determine which sex disperses. The outcome would depend upon the relative costs and benefits of dispersal versus philopatry for each sex. In red howlers, however, differences in dispersal patterns between the sexes appear to be determined by differences in the distribution of those resources most limiting to reproduction, and by conflict within each sex over access to those resources:

Females. While nearly all natal males eventually leave, female dispersal varies inversely with the number of adult females already

breeding within the troop. A female that reached sexual maturity in a troop with only one adult female (usually resulting from the death of another female) invariably bred within her natal troop, whereas a young female maturing within a troop that already contained four breeding females had virtually no chance of breeding there unless one of the adults died. The intense agonistic interactions among breeding females frequently associated with the sexual maturation and dispersal of daughters suggest that emigration is not voluntary (c.f., Crockett 1984). In those cases wherein maternity was known for more than one natal recruit, only the daughters of a single, presumably higher-ranking female were successful at remaining in their natal troops to breed. The vigorous territorial defense displayed by troop females, their aggressive exclusion of all potential female immigrants, and the high rate of injury in extra-troop migrants resulting from observed or inferred attacks by troop females (Crockett and Pope 1988) imply strong competition for breeding membership within troops.

The costs of dispersal were high. Females living outside of troops were never observed to reproduce successfully during the nine years that the population was censused. Only two females were successful at immigrating into established troops during that period, and at least one of these suffered 50% higher infant mortality than the other females in the troop. Forming a new troop with other extratroop individuals required finding an unoccupied area of suitable habitat, and was a relatively infrequent occurrence in the woodland study area. Rate of new troop formation between 1981 and 1985 was 3.5 new troops per year, and troop failure rate for those formed prior to the last six

months of the study was nearly 50%. The reproductive success of those females breeding in newly formed troops was substantially lower than that observed among females in established troops: both infant mortality and mean interbirth interval were 30% higher than the population means. Age of first reproduction for disperser females that were able to become members of new troops was significantly higher than for females that reproduced in their natal troops.

Differences in the nutrient content of those foods eaten by troop and extratroup females suggest that the array of foods available to troop animals may be higher in nutrients necessary for reproduction. The diets of troop females were significantly higher in both phosphorus and crude protein than those of extratroup females, and significantly lower in neutral detergent fiber (cell wall components). The availability of phosphorus, in particular, is extremely low in most tropical soils (Vitousek and Sanford 1986), and is frequently a limiting nutrient in domestic herbivore forage (Lloyd et al. 1978). While both nitrogen and phosphorus may be bound by plant secondary compounds that make them unavailable for digestion, there is no a priori reason to assume that troop female foods were higher in these compounds than those eaten by solitary females. Both diets included a wide array of species and plant parts, and those foods consumed by troop females had a higher overall in vitro digestibility than those of solitary females. The lower ash-free neutral detergent fiber (NDFA) content of troop female diets indicates that these foods have a significantly lower ratio of cell walls (cellulose, hemicellulose, and lignin) to cell contents (proteins, lipids, and non-structural carbohydrates such as starch and

sugars). Cell contents are easily digested by endogenous enzymes and rapidly absorbed in the small intestine, whereas cell walls must be degraded by gut microflora in the large intestine. Although microbial hindgut fermentation of cellulose and hemicellulose releases usable energy in the form of volatile fatty acids and lactate that can supplement that contained in the soluble carbohydrates, lignin is essentially non-digestible. The percentage of the NDFA comprised of lignin, and the efficiency of microbial hindgut fermentation in the red howler would both determine the degree to which the energy contained in the cell walls is made available. Differences in NDFA content may be responsible in large part for the differences in the relative digestibility of the two diets. Protein contained within cell contents that are not released until microbial breakdown of cell walls in the large intestine may be largely unavailable to the animal, since protein absorption takes place primarily in the small intestine of non-ruminants (Bjorndal 1985). Thus the protein available in the solitary female diets may be even lower relative to troop female diets than indicated by crude nitrogen content.

The effects of nutrient limitation on red howler growth and reproduction are difficult to assess because there are no estimates yet of minimum nutrient requirements for captive animals of this species. In all mammals, however, requirements for protein, phosphorus, calcium, and Kcals increase more dramatically than those for any other nutrients during gestation and lactation (Lloyd et al. 1978). The diets of solitary females were substantially lower than those of troop females in two and possibly three of these nutrients, a discrepancy that may be at

least partially responsible for the failure of extra-troop females to reproduce. Although extratroop females copulated repeatedly with both troop and extratroop males, they did not conceive. These females may not have been in estrus, which is extremely cryptic in red howlers, so whether lack of reproduction was a result of failure to come into estrus, failure to conceive, or failure to bring gestation to full term was impossible to determine.

All of the troop females sampled were nulliparous and non-pregnant, yet the nutrient quality of their diets was substantially higher than those of not only solitary females but troop males as well, who presumably had the same array of food items available to them as troop females. Troop female diets were significantly higher in crude protein and phosphorus, and significantly lower in NDFA than the diets of solitary females, solitary males, and troop males. Thus the increased dietary needs of young females may be only indirectly tied to reproduction. Since females emigrate from their natal troops at an earlier age relative to sexual maturity than males (Crockett 1984; see also below), and the troop individuals were selected to match the age and size of the solitaires, females may have been at a more active stage of growth than males. All sample females were large immatures, whereas only two of the male sample pairs consisted of immatures. The remainder were adults. Troop females may thus have been selecting higher quality food items than troop males in order to supply higher nutrient demands associated with growth. This implies that immature solitary females, who consumed diets almost identical to those of non-growing group and solitary males for all nutrient components except NDFA, would have more

difficulty meeting growth requirements than immature troop females. Since increased demands for the same nutrients limit growth as well as reproduction, an extratroop female that reaches sexual maturity after spending her last year of growth on a poor quality diet may accumulate a nutrient deficit that leaves her in poor reproductive condition.

Most females emigrated from their natal troops at two to three years of age (medium juvenile size), whereas the modal age class for natal male emigration was four to six years (subadult size; Crockett 1984). Growing daughters of adult troop females compete directly for food resources with other reproducing troop females and their offspring, and they compete indirectly with the present or future daughters of those females for the limited number of breeding positions in the troop. An adult female should attempt to coerce the daughters of other females to leave at as early an age as possible, thereby not only eliminating a direct source of competition, but precipitating interactions with potential challengers for troop breeding positions while they are still immature and unable to defend themselves. The mother of the challenged female may intervene at this point on her daughter's behalf, as was observed in troop M62 by Crockett (1984). Thus in a troop of two adult females in which 55% of maturing females emigrated, a maturing female's chances of being able to stay and breed may be primarily dependent upon the rank of her mother. Crockett and Rudran (1987b) found that females had longer than average interbirth intervals after the birth of daughters that eventually reproduced in their natal troop, and suggested that adult females may be investing more in these offspring.

By the time there were four adult females in a troop, all daughters emigrated. At this point, a daughter breeding within the troop may be detrimental to the survival of her mothers' future offspring due to competition for the limited resources available within the troop home range area, which is finite. Direct competition of this nature in a large troop may also limit the availability of those resources to the immature female herself. If a young female's chances of being able to remain in her natal troop as a breeder are small to none (i.e., troops with three to four adult females), then it would be to her advantage to begin participating in the lengthy process of new troop formation as soon as possible so that she will be in a position to breed before the onset of her first estrus. In these cases, it would be to the maturing female's advantage as well as that of the adult females in the troop that she emigrate early. All of the new troops that formed in the woodland study area contained at least one immature female, some as small as medium size juveniles. These females had the advantage of a defended resource area that could aid them in acquiring the necessary nutrients to complete their growth, as well as that of being in a position to breed without delay when they reached sexual maturity.

Adult females and their offspring also compete directly for resources with the sons of other females, but this cost may be more than offset by the benefit of increased protection afforded by large immature males from troop take-over by outside males. Subadult males, in particular, are clearly instrumental in helping the adult male to maintain breeding tenure (see Chapter 2). Since troop take-over is frequently followed by infanticide (Crockett and Sekulic 1984), and

troop stability with regard to length of male breeding tenure is positively correlated with female reproductive success (Pope and Crockett, in prep; see also Chapter 4), immature males, regardless of maternity, are a potential asset to troop females.

Males. Although virtually all males eventually emigrate from their natal troops, many remain well into adulthood (six years). Approximately 25% of the males that emigrated between 1981 and 1985 were aged six or older, and the majority of the remainder were aged between five and six years. In Chapter 2 it was demonstrated that the reproductive fitness of the breeding male was directly enhanced by the delayed dispersal of natal troop males. Natal adult, subadult, and even large juvenile males helped the breeding male in repelling attempted invasions by extratroop males. In the woodland population, single males were unable to maintain breeding tenure in troops with more than two adult females unless aided by another adult or subadult male. Natal males aided the breeding male in troop defense even in cases in which they were unrelated to him, such that the retention of both sons and non-relatives were potentially beneficial. Anecdotal evidence suggested that the breeding male may actively "encourage" natal males to stay, especially in troops with a large number of adult females.

Unlike females, there was no difference in the diets of troop and solitary males with regard to the four nutrient parameters that were measured, suggesting that intratroop competition for food resources had little influence on male dispersal. While growing males may need increased amounts of protein and phosphorus in their diets, adult males, unlike breeding females, probably do not. The demands of reproduction



for adult males are more likely to be limited by energy, or stores of useable carbohydrates, needed for competition over access to troop females. Troop invasions and status changes between males are intense, involving vigorous display as well as chasing and physical aggression that frequently results in serious injury (Rudran 1979, Crockett and Pope 1988). Curiously, the NDFA of both troop and solitary female diets were lower than that for troop males. All sample males were grown or nearly grown. It is possible that storage of the fatty acids provided by hindgut fermentation is adequate to supply the sporadic energy requirements of male competition. Time between bouts of activity may be ample to allow for the relatively slow action of cell wall decomposition accomplished by gut microflora. Also possible is that the low NDFA of the female diets was more important with regard to protein availability than energy demands (see above). Adult males were thus not as likely as females to be in direct competition with immature individuals over high quality sources of the same nutrients. Allowing natal males to remain within the troop probably costs the breeding male very little, and may greatly enhance his reproductive success.

In those troops with more than one adult male, there is some potential for competition between the subordinate male and natal males reaching maturity within the troop, particularly if the subordinate male is not related to the breeding male or the natal males. Adult males should prefer relatives as partners in two-male troops, and anecdotal evidence suggests that non-related partners are replaced by sons when possible (see Chapter 2). Those troops with two fully adult males retained fewer subadult and large juvenile males than those troops with

only one adult male, providing some evidence for natal male - adult male competition. However, both adult males and natal males in these cases have less to lose than in single-male troops if the natal male emigrates. Failure to stay may be more a consequence of mutual lack of incentive than of coercion, especially if a breeding opportunity arises nearby in the population, or if there is an opportunity to disperse with a sibling or half-sibling.

The immature male derives benefit from delaying dispersal in several ways. Until he reaches adult size, he will probably not be able to compete successfully with adult males in gaining access to breeding females. During the time when he is growing, he presumably derives the same benefits from troop membership as growing females in being able to exploit high quality sources of potentially limited nutrients. Perhaps equally important is the opportunity to take advantage of changes in local troops that leave them either more open or more attractive to invasion. Males in search of breeding opportunities appear to benefit greatly from familiarity with the local troops in their area. In the woodland study area, 86% of immigration events by males born within the population for whom time of natal emigration was known ( $n=21$ ) involved immediate transfer, with no time spent in the costly extratroup stage. The remainder of the transfers occurred when the population was not being censused regularly, and may or may not have been immediate. The closeness with which troops are monitored by local males is illustrated by two unwitting "removal" experiments that occurred during tagging operations. The first, described by Rudran (1979) and Sekulic (1983), occurred in 1978 when one of the adult males in two-male troop M74 died

from a fall. Within 24 hours, two young adult males from neighboring troop M73 invaded M74 and successfully evicted the remaining male. The second incident occurred in 1981, when the two adult males and both subadult males from troop M66 were removed from the troop simultaneously for tagging. By the next morning, the adult and subadult males from adjacent troop M75 had abandoned their troop of one adult female (one had recently died), and taken-over the undefended M66, which had four adult females. The original adult males, when released near their troop, were unable to regain tenure.

Local males may thus have an advantage over foreign males in being able to respond more rapidly to changes in surrounding troops. This may be one reason why many males that emigrate from their natal troops spend the majority of their time after dispersal within and adjacent to their natal home ranges. All three of the radio-collared males of known natal origin ranged over relatively small areas that included all or nearly all of their natal home range, and the area immediately surrounding it. This behavior was also observed in tagged males that had emigrated from troops M61 and M77, and was presumed to have occurred among those males that formed new troops adjacent to their natal troop home ranges ( $n = 6$ ). By remaining within and around their home range area, emigrant males may also benefit from familiarity with local food resources. However, the nutrient quality of foods consumed by solitary males was not any better than that of foods consumed by solitary females, who were almost certainly not familiar with their local area. Food resources may be a more important factor for males that have emigrated at an earlier stage in their physical development than adults or subadults.

Dispersal Patterns. Those resources that limit reproduction in each sex are thus distributed differently in space. Females require a dependable supply of food sources that allow them to meet the increased demands of pregnancy and lactation for nutrients that are typically in limited supply, either spatially or temporally. Competition over these nutrients within the troop territory results in the emigration of females from their natal troop. Because they are unable to transfer into established troops, those that disperse must find suitable unoccupied territory that contains adequate food resources for reproduction, as well as an association of other migrant individuals with which to form a new troop. Males must successfully take-over and defend a group of females from other males. Those females may either be members of a troop on an established territory, or an association of extra-troop females. Groups of females were distributed at intervals of approximately every 300 m, becoming more clumped beyond the boundaries of the woodland study area as trees became more patchily distributed (see Chapter 4). Unoccupied habitat that appeared suitable for colonization within the study area was nearly non-existent by the end of the study period. Troop home ranges were either completely bordered by those of other troops, or by a combination of other troops and areas of open savannah or scrub. Population density by 1981 was 112 howlers per  $\text{km}^2$ , and by 1985 was 118 per  $\text{km}^2$  (Crockett and Eisenberg 1987).

Differences in dispersal distance and ranging patterns of extratroop males and females corresponded to differences between the distribution of unoccupied feeding territory and the distribution of groups of females. Females dispersed at least six times farther than

males, travelled farther per day, and ranged over substantially larger areas. Males tended to be highly philopatric, remaining within and around their natal home range until they could transfer into a nearby troop, or form a new troop. The three radio-collared males that circulated around their natal home ranges had emigrated relatively recently. The two that had emigrated earliest, males T5 and T8, had both managed to take-over a group of females, although T8 was evicted shortly afterwards. If no success is achieved after some critical period around the natal territory, the male may begin to range over a wider area, like radio-collared male T2.

In areas that are less saturated than the woodland study site, suitable habitat for colonization by new troops will be more widely available, and breeding opportunities should increase for dispersing females. Evidence for this effect was found by Crockett (1984, 1985) in the gallery forest study population, which was undergoing a period of rapid growth between 1978 and 1981. Rate of new troop formation was more than three times higher than in the woodland population. In the gallery study area, the number of primiparous females that gave birth to their first infant in new troops was five times greater than the number that gave birth in their natal troop. In the woodland population, the opposite occurred: nearly three times more primiparous females gave birth to their first infant in their natal troops than in a non-natal troop. Dispersal distance for emigrant females should be less when rate of new troop formation is high, and increase as the amount of habitat available for colonization recedes under population expansion.

### Gene Flow and Inbreeding

Gene flow among troops within the population was almost entirely via males, since females were virtually unable to transfer into established troops, and the rate of formation of new troops that produced offspring was extremely low. Although average male dispersal distance was only one troop home range diameter, mean length of male tenure (7.5 years) was only about one third as long as their reproductive lifespan of 20 to 25 years (Crockett and Pope 1988). An immigrant male may have been born in any troop within a three home range diameter or larger radius. Also, some males dispersed farther than one home range diameter. Thus the potential origin of an immigrant allele was essentially random in relation to the size of the woodland study area. Males did not transfer preferentially from one troop to another, as has been observed in vervet monkeys (*Cercopithecus aethiops*; Cheney and Seyfarth 1983). No unilateral exchange of males among troops was observed more than once during the study period.

Local transfer of males between adjacent matrilineal will nonetheless increase the probability of inbreeding as relatives accumulate in neighboring troops. Close relatives (i.e.,  $r > .125$ ) that a male could encounter as potential mates include a half-sister, or the daughter of a full brother. The likelihood of this happening was very low since: (1) male exchange was slow relative to dispersal rate, (2) the probability of consecutive transfer between the same two troops was small, and (3) a large percentage of females emigrated from their natal troops. Indirect inbreeding with non-close relatives is inevitable under this breeding system if troop matrilineal persist long enough. There

appears, however, to be very little genetic cost associated with low - level inbreeding of this type. Wright (1921) demonstrated that repeated mating between related individuals for which  $r$  was less than 0.125 did not reduce mean heterozygosity or polymorphism in a randomly mating population. In a non-random mating system in which males are non-preferentially exchanged among matriline, Chesser (in prep.) has shown that the population inbreeding coefficient  $F_{is}$  will initially increase, but will reach an asymptote after several generations and remain constant thereafter.

Limited inbreeding associated with philopatry may benefit individual progeny by preventing the break-up of locally specific co-adapted gene complexes (Bateson 1983; Shields 1982). In a colonizing species such as the red howler monkey, this may be particularly advantageous. Red howlers range over a variety of habitat types distributed throughout a wide, topographically diverse geographic area. Locations may vary tremendously with regard to the distribution and array of food species, nutrients, secondary compounds, and potential competitors. Low success rate of new troop formation, variance in troop reproductive success, and the large genetic differences observed among troops, suggest that inter-demic selection at the level of interacting gene complexes may be a way in which red howler founding populations adapt rapidly to local conditions (see Chapter 4). Male philopatry and associated levels of inbreeding may serve to maintain these locally adapted gene complexes once they are established. Under these conditions, a male that immigrated into a local group would be more likely to produce successful offspring.

Close inbreeding in cases of extreme philopatry (i.e., natal troop males breeding with their mothers or sisters, and daughters breeding with their fathers) was not avoided when the opportunity arose. The latter, in particular, may occur with some regularity given the length of male tenure relative to female generation time. While close inbreeding of this sort is probably deleterious to reproductive fitness in terms of reduced offspring survival (Ralls and Ballou 1982, Senner 1980), it probably does not occur often enough in the population for the costs to outweigh the benefits of philopatry, especially for females. A female that reaches sexual maturity in a troop wherein her father is the breeding male can expect his tenure to change in another 2.5 years. Even if she produced no surviving offspring during this period, her age of first reproduction would be roughly equivalent to that of migrant females that were able become members of new troops, her expected mean interbirth interval would be 30% smaller, and her expected infant survivorship would be 30% higher. Increased infant mortality resulting from close inbreeding may actually be less than that observed in new troops. Those infants produced through presumed inbreeding with fathers appeared healthy and normal by the end of the study period. If the female were to emigrate, she would run the risk of reduced nutrient availability leading to poor reproductive condition, increased mortality, and possibly never being able to establish membership in a successful new troop. The variance in reproductive success among emigrant females may be as high or higher than that among males. The costs of dispersal under these circumstances would appear to far



outweigh the costs of breeding with father until another male takes over the troop.

Males risk little in breeding with daughters, since their investment in individual offspring is very small (Smith 1979). There are no alternative females to mate with besides those in the troop, so a male is no worse off if he mates with his daughter and produces no offspring than if he had not mated at all. Females prevent extratroup females from immigrating, such that evicting a daughter would only result in another daughter eventually taking her place. When a male breeds within his natal troop, the cost of inbreeding will be directly proportional to the number of adult females that he is related to in the troop. If he is related only to his mother, then he may still have one to three unrelated females as mates, which is in all cases better than none. Unless the opportunity to breed in another troop is available, his reproductive fitness in this case will be increased more by breeding in his natal troop than by emigrating. Males that do not transfer immediately after emigration may spend considerable time as extratroup animals before they are able to enter another troop and become the breeding male. In troops in which the natal male is related to all or most of the females, the costs of inbreeding will be relatively high. Even if they exceed the costs associated with dispersal, the opportunity for a male to breed in his natal troop may occur so rarely that there has been no selection for inbreeding avoidance within that context. Natal male incest may thus be an occasional artifact of strong selection for philopatry.

In either case, there is no evidence for either males or females that observed dispersal patterns arose in response to selection for inbreeding avoidance. The cost of dispersal for both sexes is high, and both appear to choose close philopatry whenever possible. Differential dispersal patterns in red howler males and females are more parsimoniously explained by intra-sexual competition for limited resources that are distributed differently for each sex.

In areas of high population density such as the woodland study site, increased competition for fewer and more sparsely distributed breeding territories may compel dispersing females to travel long distances before transfer into another troop is possible. Increased troop density in such areas will increase the number of local female groups available to males, but also the number of competitors. Some males, like radio-collared male T2, will, like females, travel far in search of breeding opportunities. One tagged male from the woodland population was found in the gallery forest approximately five kilometers from his natal troop. While locals appear to have competitive advantage over outsiders in a saturated area like the woodland, long distance immigrants may have a relatively good chance of breeding in a colonizing situation such as that observed in the gallery forest. Thus maximum density populations like the woodland serve as a source of colonizers for less saturated surrounding areas, but probably receive few successful immigrants from those areas.

### Comparisons with Other Species

In the mantled howler (*Alouatta palliata*), both males and females disperse from their natal troops (Glander 1975, 1980; Jones 1980). Unlike *Alouatta seniculus*, however, females are able to transfer into established troops after emigration. In two mantled howler troops observed by Jones (1980), females competed for troop membership at all stages of their reproductive lifespans. Younger individuals challenged older, higher ranking individuals within the troop, and sometimes formed cooperative coalitions against other females. Older, parous females as well as young nulliparous females that either dropped in rank or failed to rise in rank were observed to emigrate.

Within-troop aggression in red howler females is also observed mainly between breeding females and the maturing daughters of other females, with mothers intervening on their daughter's behalf. Curiously, this aggression seems to disappear after a natal female gives birth (Crockett 1984). No attempts were ever observed to evict a female that had already given birth within the troop, although it would seem that coalitions between mothers and adult daughters could have easily accomplished this task in those troops that consisted of a single matriline plus one other female. Red howler females control troop size by excluding all outside females and evicting natal females at an early age, whereas mantled howler females do not exclude all immigrant females, and appear to compete constantly among themselves for higher rank. Those mantled howler females that emigrated tended to be low ranking, and were both young and old. These differences between the two species may be related to differences in troop size and the degree of

relatedness among troop females, although whether they are a cause or effect is difficult to distinguish at this point. Red howler troops, with two to four adult females, will ultimately come to consist of a single matriline. Females are only added from within and new troops rarely contain more than two females, such that the more females there are in a troop, the higher the coefficient of relatedness among them is likely to be. A typical mantled howler troop contains four to eight adult females (Crockett and Eisenberg 1987), and those troops observed by Jones contained 10 and 15 adult females. These females are unlikely to be closely related to each other, given a regular cycle of emigration and immigration. In fact, mean coefficient of relatedness may go down as the number as the number of adult females in a troop increases. Females in this situation should be less likely to cooperate with each other in excluding immigrant females, especially if by forming a coalition with an outsider, a female can rise in rank. Also, the cost of emigration may be higher for red howlers because they are unable to transfer into other troops, such that even very low ranking females are better-off remaining in the troop than emigrating. Emigration may be a more viable option for low ranking mantled howler females, especially in a troop containing a large number of non-related females competing for the same limited food resources.

Routine emigration of natal troop females is rare among primates. In addition to mantled howlers, it has been described in Pan troglodytes (Wrangham 1975; Nishida 1979), Gorilla gorilla beringei (Harcourt 1978), Papio hamadryas (Sigg et al. 1982), Macaca radiata (Sugiyama 1971), and Colobus badius (Struhsaker 1975). Additional species in which female

emigration has been observed occasionally or rarely have been summarized by Moore (1984). Unlike other species in which females emigrate, red howler females do not usually transfer into other troops.

Moore (1984) suggested that female transfer species, due to lack of close kinship among troop females, should not conform to Wrangham's (1980) model of primate social evolution in which intratroup competition for resources selected for female-bonded social groups. Both Wrangham (1980) and McKenna (1979) correlated lack of kin-oriented female social groups with folivory, suggesting that this was a consequence of reduced intra-troop feeding competition associated with a relatively uniform, low quality diet. Red howlers, although they are mainly folivorous and exhibit routine female emigration, do not conform to these predictions. Two assumptions inherent in these models did not pertain: (1) despite an apparent abundance of resources, solitary female diets were comprised of foods that were significantly lower in limited nutrients than diets of troop females, and intra-troop competition was aggressive; (2) although females commonly emigrated, they were almost never able to transfer into established troops. Relatedness among adult females in red howler troops is thus potentially higher than among females in those species in which females do not emigrate, since they tend towards a single matriline instead of several (e.g., most Cercopithecines, Cebus sp.). Red howler females may be an exception that "proves" the rule, since they support Wrangham's hypotheses that intra-troop competition for resources selects for female-bonded kin groups, and that female transfer should not be observed in those species in which intra-troop competition for resources is high.

The manner in which new troop formation takes place in red howlers provides evidence for a mating system in which females cooperatively defend resources, and males defend access to female groups ("cooperative female choice," Altmann et al. 1977; see also Emlen and Oring 1977, and Wittenberger 1980). Extra-troop associations of mixed sex invariably revolved around two or more females that were observed with a series of different males or combination of males. The associations that developed into two of the three new troops formed in 1982 were observed extensively during 1981. In both cases, associations of females showed a high degree of site-specificity, remaining for six months or more within the area that eventually became the troop home range (or part of it). At least three different males were observed affiliating at different times with each female association, none of which eventually became the breeding male in either of the two troops. In a third case, a newly formed troop failed, leaving only two adult females and a small juvenile male. All three remained within and around the old territory originally occupied by the troop for four months until one of the females came into estrus. At this time they were joined by an extra-troop adult male, who was eventually evicted by radio-collared male T5. Male T5 remained with the females in their old home range for the remainder of the study period, and was eventually joined by a subadult male with whom he occasionally associated prior to the take-over.

These female groups were clearly not choosing territories defended by males. Two of the three spent considerable time during which no male was associated with them at all. While they may have been able to exercise female choice by failing to cooperate with a particular male,

they could not prevent a male from aggressively excluding other males from the ranging area. Female lack of choice with regard to the males that associate with them is amply demonstrated by the inability of females to prevent troop take-over and associated infanticide. Females frequently avoid cooperating with new males after troop take-over (Sekulic 1981; Crockett and Sekulic 1984), but are apparently unable to influence the outcome of male competition over troop access.

CHAPTER 4  
THE INFLUENCE OF RED HOWLER SOCIAL STRUCTURE  
ON GENETIC MICRODIFFERENTIATION WITHIN AND BETWEEN  
POPULATIONS

Introduction

Studies examining the effects of social structuring on the distribution of genetic variation among geographically discrete populations have focused largely on its influence on effective population size, and the degree to which this may foster inbreeding and genetic drift among demes (e.g., Karlin and Campbell 1980; Wright 1921, 1938, 1946). The genetic consequences of the rate and pattern of dispersal by individuals among demes have been described by numerous isolation by distance models in which the cohesive effects of migration are counterbalanced by drift and mutation. These are basically of the familiar island model type described by Wright (1943), or the stepping stone model in which gene flow is limited to adjacent demes arranged in a geometric configuration (Kimura 1953; Kimura and Weiss 1964; Malecot 1955).

More recently, these models have been extended toward examining the genetic structure of populations in which the basic unit of evolutionary interest is the social group. In most socially structured vertebrate populations this is the smallest unit of individuals among which random breeding can be assumed to take place. The comparative



genetic isolation of such units results from socially mediated constraints on gene flow such as territoriality, presumed inbreeding, and small effective population size. These processes have been proposed to foster drift and genetic heterogeneity among social groups that may enhance rates of evolutionary change in social species (Bush 1975; Wade 1982; Wilson et al. 1975; Wilson 1983 ).

Although variable amounts of genetic heterogeneity among social units have been demonstrated in a handful of species, the mechanism remains unclear. In marmots, Schwartz and Armitage (1980) found highly significant genetic divergence among colonies despite observed high rates of gene flow and absence of potential inbreeding. Heterozygosity of individuals relative to colony allele frequencies was higher than expected. Chesser (1983), conversely, found high levels of genetic variation among prairie dog coterries accompanied by lower than expected heterozygosity of individuals relative to coterries, but had no demographic data on genetic exchange among groups. Demographic studies have presented evidence that close inbreeding, and certainly indirect inbreeding based on limited vagility, may be more common than previously thought in many social species (Shields 1982, 1986). Genetic differentiation among social units, however, has generally been found to be accompanied by some degree of heterozygosity within groups in excess of isolation model predictions (e.g., Melnick et al. 1984; Neel and Ward 1972). Specific demographic data on accompanying rates of intergroup migration have not been reported for these studies.

Clearly, models based on genetic isolation are not adequate to explain the patterns of gene diversity observed within socially

structured populations. Why some species should display greater genetic divergence between social units than others is not evident based on presumed gene flow. The manner in which this mechanism operates is critical to an evaluation of theories proposing that structuring of populations into discrete social groups may have accelerated their rate of evolutionary change, either through drift accompanied by interdemographic selection (Wade 1982; Wilson 1983), or by promotion of genetic isolation through fixation of chromosomal variants (Bush 1975, Wilson et al. 1975; White 1968).

Red howlers are an herbivorous species of New World primate that have been characterized as a colonizing, or pioneer species (Eisenberg 1979). Their geographic range extends over the northern 25% of the South American continent, wherein they are found in a wide variety of habitats ranging from the deciduous riparian forests of Manu (Terborgh 1983), to Andean cloud forest (Gaulin and Gaulin 1982), to the scrub-woodland savannah of the lowland Venezuelan llanos (Braza 1980). Troop size and composition remains consistent throughout their range (Crockett and Eisenberg 1987). Their social structure is typical of that exhibited by most primate species with two exceptions: females may emigrate from their natal troops (Crockett 1984; Crockett and Pope 1988), and new troop formation does not occur through lineal fission (see Chapter 3). The demography of the red howler population at Hato Masaguaral has been monitored for over twelve years, various aspects of which have appeared in numerous publications (see below). This report is based on ten years of data from 1975 - 1985.

The purpose of this study was to determine the genetic structure within and between red howler populations, and to examine how these findings are correlated with observed rates and patterns of gene flow. Partitioning of genetic variance among troops, and among genealogical subsets of troops defined by the non-random distribution of genomes among the breeding units, are compared to observed migration rates. The correlations between genetic and geographic distances among troops are examined. These results are compared to those reported for other species in order to determine what general conclusions can be drawn about the relationship between social organization and genetic structuring of populations. Finally, models describing the influence of social organization on rates of evolutionary change are evaluated based on these findings.

### Methods

#### Study Population

The study area was Hato Masaguaral, a cattle ranch and wildlife preserve located in the central llanos of Venezuela. The western portion of the ranch is comprised of semideciduous open woodland interspersed with small patches of scrub and open savannah, while the eastern part is occupied by a dense, semideciduous gallery forest associated with the Rio Guarico and a large stream, the Cano Caracol. These two habitats are described in detail elsewhere (e.g., Rudran 1979; Troth 1979; Crockett 1985). The western woodland is a geographically circumscribed area of howler habitat bordered on the north and south by extensive agricultural development, and on the west by open, seasonally inundated palm savannah (estero, Troth 1979). This area is separated

from the gallery forest by a wide swath of open savannah, 4 km wide at its closest juncture, that is unoccupied by howler troops. The gallery forest is part of a continuous, narrow corridor of howler habitat extending along the Rio Guarico from the Guarico Dam 60 km north of the ranch, to the Rio Apure 75 km to the south, where the two drainages join.

In 1975, John F. Eisenberg initiated a long term study of red howler demography at Masaguaral. Howlers living in the western and eastern portions of the ranch were considered to be two distinct populations with some unknown amount of genetic migration taking place between them. Western woodland troops were censused by John Eisenberg and Devra Kleiman in 1975 (Crockett and Eisenberg 1987), by Rasanayagam Rudran in June and July of 1976, and from January 1977 through October 1978 (Rudran 1979), by Carolyn M. Crockett from March 1979 through February 1981, and by the author throughout 1981, 1984, and the first seven months of 1985, with an annual census by Crockett in 1983 (Crockett 1985; c.f., Chapter 3). Gallery troops were censused by K. Green in 1975; and by Crockett in October 1978, March 1979 through February 1981, December 1981, February 1983, February 1984, and March 1987 (Crockett 1985). Early censuses of both populations were made in 1969 by Neville (1972). The number of woodland troops censused grew from 14 in 1975 (J. F. Eisenberg, pers. comm.) to 33 in 1985 as additional troops were discovered at the periphery of the study area, or were newly formed within. Gallery troops censused by Green in 1975 were at eight. Gallery censuses by Crockett grew from 14 in 1978 to 23 in 1984 (Crockett 1985).

In March 1978 (Thorington et al. 1979), and during January and December 1981, 194 howlers were captured (see below) and marked with unique patterns of colored ear tags that insured positive identification of individuals after dispersal. Many additional animals in the population were individually recognizable by characteristics such as skin depigmentation patterns, missing digits, permanent scars, and torn ears and lips.

The information that has resulted from these 10 years of demographic data, in addition to the results of studies done on paternity exclusion (see Chapter 2), and dispersal ranging patterns (see Chapter 3), have made possible the direct measurement of patterns of gene flow within and between populations, effective population size, and levels of inbreeding within populations, which are summarized below.

#### Population Structure

Average home range size was 5.5 ha in the woodland population (Crockett 1985; Sekulic 1982) and 25 ha in the gallery forest (Crockett 1985). The distribution of troops within the study areas was relatively uniform, with considerable home range overlap, such that mean distance between the centers of adjacent home ranges was 275 m in the woodland habitat, and 368 m in the gallery (based on Crockett 1985).

Troop size ranged between 4 and 16 individuals per troop. Both populations increased in size during the course of the 10 year study period (Crockett and Eisenberg 1987, Table 6.5), but the magnitude of this change was much larger in the gallery, which had apparently undergone a severe population crash several years prior to the onset of the study in 1975 (Table 11). Mean troop size in the gallery population

dropped from 9.6 in 1969 (Neville 1972) to 4.6 in 1977 (Rudran 1979). The reasons for this decline are unknown, since there were no censuses made during the intervening years. By 1984, mean troop size had increased to 7.8 (Crockett 1985). Population density in the gallery area rose from 36 howlers/km<sup>2</sup> in 1981, to 53 howlers/km<sup>2</sup> in 1984 (Crockett and Eisenberg 1987).

Mean troop size in the woodland population increased from 8.5 in 1969 (Neville 1972) to 10.5 in 1981 (Crockett 1984), but had decreased to 9.5 by 1985. The decrease in average troop size during these last 5 years was caused by the large number of new troops, typically smaller than established troops, that arose in this population between 1983 and mid-1985 (Table 10). Population density in the woodland area rose steadily throughout the study period, increasing from 83 howlers/km<sup>2</sup> in 1969 to 118 howlers/km<sup>2</sup> in 1984 (Crockett and Eisenberg 1987). In both populations, once the mean number of individuals per troop reached between 8 and 9, mean troop size remained stable or decreased slightly, despite continued increases in population density (Table 11).

#### Effective Population Size $N_e$

Troop  $N_e$ . The troop is the smallest unit in the population that mates approximately at random. Mean annual number of adult males per troop ranged from 1.5 to 1.7 in the woodland population, and from 1.1 to 1.2 in the gallery (Crockett and Eisenberg 1987). Observations of copulations in multi-male troops (Sekulic 1983; c.f., Chapter 2) and paternity exclusion using genetic markers (see Chapter 2), indicate that all or most offspring in a multi-male troop are fathered by only one of the males (i.e., in no case could the male genetically identified

Table 10. Observed gene flow among troops. Mean home range diameter (hdr) is 275 meters.

	Male	Female
Dispersal from Natal Troop	100%	73%
Mean 1 <sup>st</sup> Time Dispersal Distance	1 hrd*	6 hrd
Mean 2 <sup>nd</sup> Time Dispersal Distance	1 hrd	_____
Mean Lifetime Dispersal Distance	3 hrd	6 hrd (Dispersers Only)
Migration Rate (= mean male tenure length)	7.5 yrs = 0.67 males/gen	Remain in Breeding Troop for Reproductive Lifespan
Effective Migration Rate N <sub>m</sub> e	1 male/gen	_____

\* hrd = one home range diameter

Table 11. Calculation of effective population size for troops and geographic study area.

Population	Year	Sex-Ratio $N_e$ Troops	Area 85 <sup>th</sup> % Dispersal Neighborhood	Sex-Ratio $N_e$ w/in 85 <sup>th</sup> % Dispersal Neighborhood	Temporal Variance
Woodland	1969	2.8	3.14 km <sup>2</sup>	59.3	All Years
	1975	2.9		64.4	73.0
	1981	3.0		81.9	1981-1985
	1985	2.9		96.7	88.7
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Gallery	1981	2.8	5.50 km <sup>2</sup>	78.6	84.3
	1985	2.8		90.7	



as fathering the majority of troop offspring be excluded from fathering the remainder). Asynchronous breeding (Crockett and Rudran 1987) and long interbirth intervals of 16.6 months (Crockett and Sekulic 1984) among the 2 to 4 adult females that occupy a typical troop facilitate monopolization by the alpha- male of each female as she comes into estrus. All troops in the population were therefore considered to operate as single male harems.

Effective population sizes for individual troops were calculated using the formula

$$N_e = (4 N_m N_f) / (N_m + N_f)$$

(Wright 1938) for unequal numbers of male and female breeders. Values ranged from a minimum of 2.67 for a troop with 2 breeding females, to a maximum of 3.2 for a troop with 4 breeding females. Average sex-ratio  $N_e$  for troops varied very little from year to year, either within or between populations, regardless of differences in population density (Table 11).

Population  $N_e$ . The calculations described below are based on values reported by Crockett and Eisenberg (1987, Table 6.5), and on my census data for 1981, 1984, and 1985, unless stated otherwise. Effective population sizes for the woodland and gallery populations were estimated by first calculating the sex-ratio  $N_e$  within each population at intervals that approximated the 5 year generation time as closely as possible with the available data. The density of breeding males was considered to be equal to the number of troops per km<sup>2</sup>. The density of

breeding females was obtained by multiplying the number of troops per  $\text{km}^2$  by the average number of females per troop for the given year. The area encompassed within the 85<sup>th</sup> percentile dispersal distance (Chepko-Sade et al. 1987) was then calculated for the woodland population using the dispersal data from Chapter 3.

An approximation of 85<sup>th</sup> percentile dispersal distance area in the gallery population was obtained by assuming that dispersal distances in the two populations are directly proportional to distances between the centers of troop home ranges. Since distances between gallery troops are 1.34 times larger than distances between woodland troops (see above), the woodland 85<sup>th</sup> percentile dispersal distance was multiplied by this factor to obtain the radius of the gallery 85<sup>th</sup> percentile dispersal distance area. The sex-ratio  $N_e$  within these dispersal areas was calculated for each of the roughly 5 year generation intervals. The harmonic mean of these values was obtained for each population using

$$1/N_e = 1/t \sum N_i$$

(Wright 1938), where  $N_i$  is the sex-ratio  $N_e$  within the 85<sup>th</sup> percentile dispersal area for each of the  $t$  generations represented (Table 11).

#### Gene Flow Within and Between Populations

Data on dispersal patterns and migration rates used in this section are derived from Chapter 3.

Within Populations. The only source of immigration into troops was replacement of the breeding male through aggressive invasion by one or more outside males, only one of which would eventually breed (see

Chapter 2). The mean rate of breeding male replacement within troops was one male every 7.5 years, or 0.67 males per generation time of five years. Since the immigrant individual in this case will contribute one half the genetic complement of the following generation, the proportion of genes introduced into a troop that came from a migrant in generation  $t-1$  is  $m_e = (0.5)(0.67) = 0.33$ , where  $t$  is the generation of interest, and  $m_e$  is the effective migration rate. The effective number of immigrants per generation was calculated using the mean troop  $N_e$  of 2.9 individuals (Table 11), such that  $N_e m_e = (2.9)(0.33) = 0.96$ , or one individual per generation.

This interpretation of effective migration rate differs somewhat from Wright's  $m_e$ , in which the number of immigrants each generation is assumed to be directly proportional to their representation in the gene pool of the succeeding generation,

$$m_e = m [(q_d - q_i) / (q_d - q_t)]$$

(Wright 1969), where  $m$  is the proportion of the deme population that consists of immigrants,  $q_i$  is the gene frequency in the immigrants,  $q_d$  is the gene frequency in the deme, and  $q_t$  is the average gene frequency in the total population. This formulation adjusts for non-random exchange of immigrants among demes in a population broken-up into numerous small subpopulations in which the majority of immigrants will come from neighboring demes with similar gene frequencies. When  $q_i = q_t$ , non-random immigration effects are absent, and  $m_e$  reduces simply to  $m$ . This was the case observed in the red howler study populations, in

which genetic exchange of migrant males among troops was approximately random. Although an immigrant howler male was most likely to have come from a neighboring troop (see below), he was not necessarily born in that troop from which he emigrated. A male may successfully invade a new troop two to three times during his reproductive lifespan (Rudran 1979), such that a new breeding male may have been born in any troop within a minimum radius of three home range diameters away. There was no evidence of non-random exchange of natal males among neighboring troops, as has been described in vervet monkeys (Cheney and Seyfarth 1983): in no case did unilateral exchange of males between any two given troops occur more than once during the ten year study period. The gene frequencies of immigrants into troops were therefore considered to be representative of the average gene frequencies within the total population.

A dispersing male could enter a new breeding situation either by successfully invading an existing troop, or by forming a new troop with other solitary dispersers. The mean distance travelled by a male immigrating into a troop from the troop in which he originated was one home range diameter, regardless of which means of attaining breeding access was achieved. This was the case both for those males leaving the troops in which they had been born (first-time dispersers), as well as for those males leaving troops into which they had immigrated (second or more time dispersers). Given a mean tenure length of 7.5 years, and an estimated reproductive lifespan of 20 years (Crockett and Pope 1988), mean lifetime genetic migration distance for males was estimated to be three home range diameters (Table 11).

A male maintaining an average tenure length of 7.5 years may be presented with the opportunity to breed with a daughter, who would reach sexual maturity at 4.5 years of age (Crockett and Rudran 1987). Probable inbreeding was observed in all three cases in which a female reached sexual maturity and bore offspring within the troop in which her father still held breeding tenure. This was probably a relatively infrequent occurrence, however, since only one half of the offspring born to the females in a troop were daughters, and only one half of these would remain in their natal troop to breed.

The breeding females within an established troop eventually come to form a single matriline. Although the females in a newly formed troop (usually 2) were not always related to each other at the troop's inception, usually only the daughters of the highest ranking female were successful at remaining in their natal troop to breed (see Chapter 3). The remainder emigrated. Seventy three percent of the immature females marked in 1981 that had reached sexual maturity by the end of the 1985 study period had emigrated from their natal troops. Unlike males, however, migrant females were almost never able to immigrate into established troops. Troop females aggressively excluded migrant females by cooperatively chasing, attacking, and frequently injuring any extra-troop females encountered within the troop home range area (Rudran 1979; Crockett 1984; Crockett and Pope 1988).

Dispersing females were able to reproduce only by forming a new troop with other solitary migrants. Mean dispersal distance among those females that emigrated from their natal troops was approximately six home range diameters from place of birth to place of first reproduction.

Once a female was able to achieve breeding status within a troop, she could expect to remain there throughout her reproductive lifespan.

The majority of dispersing females left the study area. Solitary females in the woodland population ranged over an mean area that was over three times larger than that covered by solitary males, and they travelled significantly farther in their daily movements. This result is consistent with the fewer breeding options available to dispersing females. Successful new troop formation required locating other solitary dispersers of both sexes with which to form social bonds, and finding an unoccupied area of suitable howler habitat in which to develop a territory. New troop formation was a rare event in the woodland population prior to 1984, but was relatively common in the growing gallery population (Table 10). Only 13% of the female founders of new troops that formed in the woodland population since the 1981 tagging had been tagged as juveniles within their natal troops in the woodland study area. Females immigrating from outside of the study area could have originated in troops on the periphery of the woodland habitat that were not part of the study population, or possibly in the gallery forest.

Between populations. Migration of howlers from the woodland population to the gallery forest was estimated to be 12 individuals per generation, based upon the percentage of marked dispersers sighted that had relocated. This value was used as an estimate of  $N_m$ , the genetic migration rate between populations (Wright 1978). Realized  $N_m$  was probably somewhat lower, since dispersal of marked howlers from the gallery to the woodland was not observed, possibly due to the lower

population density in the gallery study area. Also, not all immigrants will be able to reproduce successfully. No relocated animals, for example, were observed as members of troops (Crockett 1985).

#### Analysis of Genetic Structure

In January and December 1981, 175 howlers from the woodland and gallery populations were captured using a CO<sub>2</sub> rifle and tranquilizer darts loaded with 10-20 mg/kg body weight Phencyclidine. Details of the capture and darting procedure are described elsewhere (Thorington et al. 1979; c.f., Chapter 2). Attempts were made to capture entire troops whenever possible. Blood samples were taken from 137 of the captured animals, representing 14 woodland troops and 4 gallery troops. The blood samples were separated into serum and hemolysate components, and frozen in liquid N<sub>2</sub> until electrophoresis was performed (see Chapter 3).

Standard starch gel and polyacrylamide techniques were used to examine 29 loci. Buffer systems and staining procedures were those described by Harris and Hopkinson (1976), unless otherwise noted. Ten loci were polymorphic: phosphogluconate dehydrogenase (6PGD), purine nucleoside phosphorylase (PNP), adenylate kinase-1 (AK-1), adenosine deaminase (ADA), glucose phosphate isomerase (GPI), peptidase C (PEP C), peptidase D (PEP D), malic enzyme (ME; Selander et al. 1971), transferrin (Tf; Altland et al. 1981; McClellan 1982), and an unidentified serum protein (SER-1; see Chapter 3). Mercaptoethanol (10  $\mu$ l per ml) was added to hemolysate samples analyzed for ADA, PEP C, and PEP D in order to prevent the formation of sulphhydryl group oxidation products and the resulting secondary banding problems associated with

them (Harris and Hopkinson 1976). Serum samples analyzed for transferrin were first saturated with iron chloride following the technique described by Altland et al. (1981). No genetic polymorphism was found in sorbitol dehydrogenase (SORDH), malate dehydrogenase (MDF), NADH diaphorase (DIA), phosphoglucomutase-1 (PGM-1), phosphoglucomutase-2 (PGM-2), red cell acid phosphatase (ACP), mannophosphate isomerase (MPI; Nichols et al. 1973), fructose bi-phosphate aldolase (ALD), carbonic anhydrase-1 (CA-1), lactate dehydrogenase-1 (LDH-1), lactate dehydrogenase-2 (LDH-2), peptidase A (PEP A), peptidase B (PEP B), esterase A (EST A), esterase B (EST B), esterase D (EST D), serum cholinesterase (CH-E), hemoglobin (Hb), or superoxide dismutase (SOD).

Proportions of genotypes at each locus were in agreement with Hardy-Weinberg expectations (chi-square goodness of fit test,  $p > .05$  for all loci). Genotype frequencies for each polymorphic locus were tested for correlation with age, sex, dispersal (vs. non-dispersal), troop status, and breeding success. No correlation was found for any locus except transferrin, at which males exhibited a significantly higher frequency of the less common allele than females. This locus was eliminated from genetic differentiation analyses.

Partitioning of genetic variance within and between populations was analyzed using Wright's F statistics (1965), incorporating those modifications proposed by Nei (1977). Expected genotype frequencies were calculated using Levene's (1949) correction for small sample size. Heterogeneity among population subdivisions was tested for significance at each locus using the Pearson chi-square contingency table analysis



with  $(s-1)(k-1)$  degrees of freedom, where  $s$  is the number of populations and  $k$  is the number of alleles. This technique yields results identical to those obtained using the computational formula of Workman and Niswander (1970) with  $F$  values calculated using weighted means and variances (Chesser 1983). Correlation between uniting gametes within population subdivisions ( $F_{IS}$ ) was tested for significance at each locus using the chi-square statistic,

$$\chi^2 = N F_{IS}(k-1)$$

with  $k(k-1)/2$  degrees of freedom (Li and Horvitz 1953), in which  $N$  is the total number of individuals, and  $k$  is the number of alleles. This statistic is not applicable to  $F_{IS}$  values averaged over loci, for which it was not possible to test for significant divergence from zero (but see below).

Given the high level of heterozygosity exhibited by individuals in the population ( $H = 0.10$ ), and the small size of troops, it was necessary to determine whether observed mean genetic heterogeneity values among troops could be arrived at through random grouping of individuals alone. A bootstrap procedure was used to create frequency distributions against which the  $F$  statistics could be compared. All individuals in the population were randomly assigned to 18 groups of the same sizes as those in the sample, and the weighted mean  $F_{ST}$  value was calculated. This procedure was repeated 1000 times, and the observed value compared to the resulting frequency distribution. Results were considered to be significant when the probability of obtaining the

observed value by chance was less than 5 trials per 100 ( $\alpha = 0.05$ ). The same procedure was used to test for significance of the weighted mean  $F_{IS}$  among troops.

The contribution of matrilineal effects to correlation among uniting gametes within troops was assessed by examining partitioning of genetic variance among breeding females. Wright's  $F$  statistics were calculated for the same troops composed of their respective breeding females only. Significance of mean  $F_{ST}$  and  $F_{IS}$  values was determined using the bootstrap procedure described above.

Presence or absence of clinal effects was assessed both within and across loci. Genetic distances among troops were calculated using Roger's modified  $D_t$  (Wright 1978). A cluster analysis based on these data was then performed using the unweighted pair group method with arithmetic averaging (Sneath and Sokal 1973). Genetic distances were compared to geographic distances between troops using Mantel's matrix correlation methods (Mantel 1967). Allele frequencies at each polymorphic locus were tested for association with geographic distance using the autocorrelation methods described by Sokal and Oden (1978a,b), with a patch size of 400 meters.

## Results

### Effective Population Size

Results of effective population size calculations are reported in Table 11. Sex ratio  $N_e$  for individual troops changed very little from year to year, despite increases in population density in both study areas. Although troop size increased, this was accomplished through the addition of immature offspring and one to two adult females, which have

relatively little effect on sex ratio  $N_e$  if the number of breeding males remains one. Sex ratio  $N_e$  per  $\text{km}^2$  for populations, however, increased steadily with population density, responding to increases in both the mean number of females per troop and the number of troops per unit area. The area of the 85th percentile dispersal distance was 1.75 times larger in the gallery than in the woodland population. Since the effective population density in the gallery was lower than in the woodland, the resulting sex ratio  $N_e$  within the 85<sup>th</sup> percentile dispersal area was approximately equal in the two study populations for 1981 and 1984/85. The population temporal variance  $N_e$  in the woodland population was lower than in the gallery because accurate data for the lower population density years of 1969 and 1975 were available only for the woodland study area.

#### Polymorphism and Heterozygosity

Allele frequencies of the 10 variable loci, percent polymorphism, and mean heterozygosities based on 29 loci are reported for all troops in Table 12. The woodland and gallery population totals were calculated for individuals in each geographic area without regard for troop subdivision. Mean heterozygosity within troops ranged from 0.057 to 0.135, and polymorphism from 17.2% to 31.0%. Mean heterozygosity in the woodland population was 0.106, and in the gallery population was 0.089. Polymorphism in the woodland and gallery populations was 34.5% and 31.0%, respectively. The overall mean heterozygosity of 0.099 is among the highest recorded for mammals (Nevo 1978; Selander and Johnson 1973). Mean polymorphism for mammals is 14.7%, and for vertebrates 17.3% (Nevo 1978), which is about half that exhibited by red howlers at Masaguaral.

Table 12. Allele frequencies at 9 variable loci.

Troop / Population	N	CEXD 100	FRP 100	ADA 100	GPI 100	PEP-3 100	PEP-4 100	HE 100	AK 100	AK 150	AK 180	PRO-1 95	PRO-1 90	H	P
<b>Woodland</b>															
M51	3	1.000	1.000	0.600	0.833	0.833	1.000	1.000	1.000	0.000	0.000	0.333	0.667	0.000	0.090
M52	8	1.000	1.000	0.688	1.000	0.813	0.813	0.875	0.875	0.125	0.000	0.813	0.188	0.000	0.077
M57	5	1.000	0.700	1.000	1.000	1.000	1.000	1.000	0.700	0.200	0.100	0.125	0.875	0.000	0.056
M58	3	1.000	1.000	0.167	0.500	1.000	0.667	1.000	0.833	0.000	0.167	1.000	0.000	0.000	0.090
M61	9	1.000	0.778	0.667	0.611	0.667	1.000	0.611	1.000	0.000	0.000	0.444	0.556	0.000	0.103
M62	9	1.000	0.688	0.889	0.889	0.889	1.000	0.778	0.889	0.000	0.000	0.444	0.556	0.000	0.103
M63	10	1.000	0.950	0.750	0.700	0.950	1.000	0.444	0.850	0.150	0.000	0.889	0.111	0.000	0.039
M64	8	0.938	0.938	0.588	0.813	1.000	0.929	0.813	0.929	0.071	0.000	0.438	0.563	0.000	0.088
M66	9	0.833	0.889	1.000	0.500	1.000	0.889	0.944	0.875	0.125	0.000	0.556	0.444	0.000	0.091
M71	7	1.000	0.714	0.643	0.714	0.571	0.929	0.500	0.833	0.167	0.000	0.750	0.250	0.000	0.125
M72	9	1.000	0.778	0.389	0.278	0.722	1.000	0.375	0.833	0.157	0.000	0.750	0.250	0.000	0.106
M75	9	1.000	0.889	0.389	1.000	0.944	1.000	0.944	0.813	0.188	0.000	0.500	0.500	0.000	0.057
M78	9	1.000	0.500	1.000	1.000	0.278	0.722	0.833	0.944	0.056	0.000	0.688	0.313	0.000	0.096
M79	8	1.000	0.938	0.813	1.000	0.625	1.000	0.563	0.875	0.125	0.000	0.563	0.438	0.000	0.106
<b>Gallery</b>															
G6	4	1.000	1.000	0.750	0.875	0.875	1.000	0.375	0.875	0.125	0.000	0.250	0.750	0.000	0.077
G7	4	1.000	0.875	0.625	0.875	0.875	0.150	1.000	0.833	0.167	0.000	0.167	0.833	0.000	0.103
G20	8	1.000	0.938	0.813	1.000	0.714	1.000	1.000	1.000	0.000	0.000	0.214	0.786	0.000	0.036
G21	8	1.000	0.667	0.833	0.667	0.800	0.750	0.750	0.875	0.125	0.000	0.667	0.333	0.000	0.112
<b>Total</b>															
Woodland	108	0.981	0.829	0.707	0.764	0.790	0.933	0.736	0.878	0.104	0.020	0.620	0.365	0.015	0.092
Gallery	22	1.000	0.864	0.773	0.884	0.800	0.881	0.810	0.921	0.079	0.000	0.350	0.650	0.000	0.077

### Genetic Variation Within and Between Populations

Genetic differentiation among troops within the woodland and gallery populations was substantial (Table 13). Allelic variance among combined troops, and among woodland troops alone, was significantly different from zero at all loci except AK-1. Mean genetic differentiation among woodland troops was 22.5% ( $F_{ST} = 0.225$ ;  $p < .001$ ), which is one of the highest values ever recorded for natural populations over such short geographic distances (Table 18). Genetic differentiation among gallery troops was less ( $F_{ST} = 0.142$ ;  $p < .001$ ), and variation at individual loci was significant only at SER-1 and ME. This was most likely attributable to the smaller sample size from the gallery, both in terms of number of individuals and number of troops, and to the young, unstable breeding structure produced by the bottleneck that the gallery population underwent between 1969 and 1975. The amount of the total genetic variance due to troop subdivision was 21.6% ( $F_{ST} = 0.216$ ;  $p < .001$ ), such that on average, only 78% of the total gene diversity could be found in any given troop. Results of the bootstrap analysis (Figure 11) indicate that the probability of arriving at this result by random small grouping effects is less than 0.001.

Variance of gene frequencies between woodland and gallery subpopulations was much lower than the variance within (Table 14). Only 2% of the total genetic variation was accounted for by differences between subpopulations ( $F_{ST} = 0.021$ ;  $p < .06$ ). Allelic variance was significant only at SER-1 ( $p < .01$ ). The second 6PGD allele and two other rare alleles: AK 180, and SER1-150 (Table 12), were present only

Table 13. F-statistics for variable loci for troops within populations and for all troops combined. Asterisks refer to significance levels associated with chi-square values: \*p < .05; \*\*p < .01; \*\*\*p < .001.

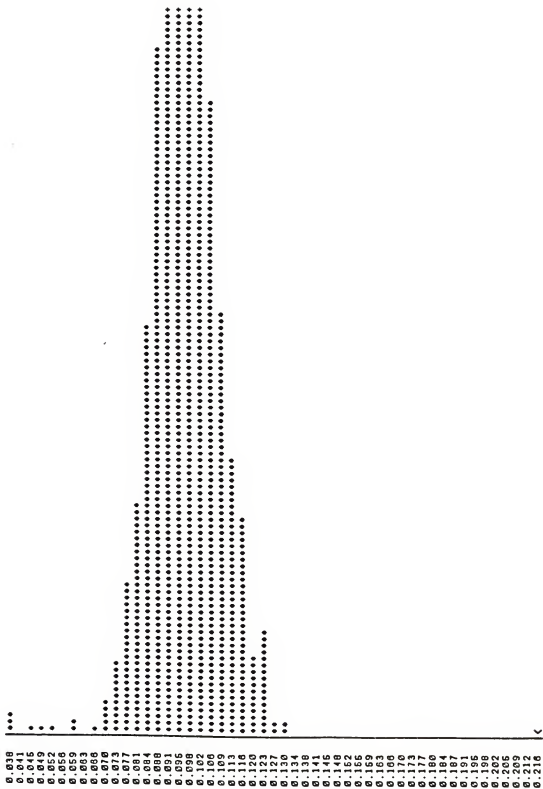
POPULATION	LOCUS	$F_{IT}$	$F_{IS}$	$F_{ST}$
Woodland (14 troops)	6PGD	-0.017	-0.160	0.124 *
	PNP	0.110	-0.055	0.157**
	AK-1	-0.116	-0.189 *	0.062
	ADA	0.094	-0.254 **	0.278 ***
	GPI	0.105	-0.251 **	0.285 ***
	SER-1	0.088	-0.173	0.222 ***
	PEP-C	0.199	-0.091	0.266 ***
	PEP-D	-0.081	-0.305 **	0.171 **
	ME	0.237	-0.021	0.252 ***
Mean		0.100	-0.161	0.225 ***
Gallery (4 troops)	PNP	0.218	0.092	0.139
	AK-1	-0.116	-0.165	0.042
	ADA	-0.324	-0.373	0.036
	GPI	-0.171	-0.323	0.115
	SER-1	0.538	0.435 *	0.182 *
	PEP-C	0.346	0.326	0.029
	PEP-D	-0.143	-0.333	0.143
	ME	0.086	-0.481 *	0.383 **
Mean		0.087	-0.064	0.142 **
All Troops (18 troops)	6PGD	-0.013	-0.060	0.127 *
	PNP	0.132	-0.026	0.154 **
	AK-1	-0.115	-0.184 *	0.059
	ADA	0.016	-0.283 **	0.233 ***
	GPI	0.040	-0.262 **	0.239 ***
	SER-1	0.228	-0.043	0.260 ***
	PEP-C	0.262	0.055	0.219 ***
	PEP-D	-0.094	-0.314 **	0.167 **
	ME	0.205	-0.105	0.280 ***
Mean		0.110	-0.136	0.216 ***

Table 14. F-statistics for variation between woodland and gallery populations at each variable locus. Asterisks represent significance of chi-square values; \*\*P < .01.

LOCUS	$F_{IT}$	$F_{IS}$	$F_{ST}$
6PGD	-0.010	-0.019	0.010
PNP	0.139	0.137	0.002
AK-1	-0.102	-0.106	0.004
ADA	-0.077	-0.083	0.006
GPI	0.052	0.036	0.016
SER-1	0.349	0.296	0.076 **
PEP-C	0.313	0.313	0.000
PEP-D	-0.102	-0.111	0.008
ME	0.142	0.135	0.008
Mean	0.126	0.107	0.021

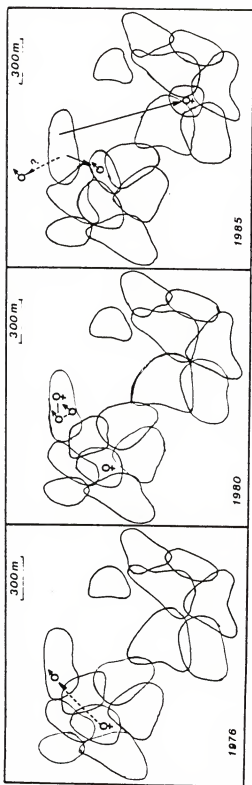
Figure 11. Histogram of bootstrap  $F_g$  results for troops within population. Probability that observed value of 0.216 is due to random grouping effects is less than 0.0001.



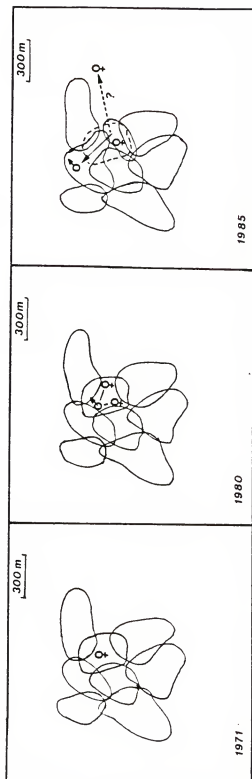


in the woodland population. The distribution of these alleles among troops corroborates dispersal data on patterns of gene flow, and gives an indication of the rate at which new alleles may spread through the population. The 6PGD-150 allele was found only in old adult female 6421 in troop M64 (dead by October 1984), breeding male 6611 in troop M66 two home range diameters away, and three of his offspring: one male and two females. The male offspring dispersed from M66 and immigrated into M82 one home range diameter away, where he remained as the subordinate male until the end of the study period. One female offspring emigrated out of the study area, and the second became a breeding female in newly formed troop M70 four home range diameters away (see Figure 12). She had produced two offspring by the end of the study period. It seems likely that male 6611 originated in troop M64, given his age compared to female 6421's, the rarity of the allele (only these two individuals prior to the birth of his offspring), and the fact that the distance between the two troops corresponds to first time dispersal distance for males. He had to have been a minimum of six years old at time of reproduction, placing his latest possible date of birth in mid-1969. Female 6411 produced no more surviving offspring from 1975 until she died. Thus over a span of at least 16 years (approximately three generations), allele 6PGD-150 had travelled a maximum of 3.5 home range diameters (959m) within the study area from M64, its probable place of origin within the population. Assuming those 6PGD-150 individuals that left the study area travelled the mean dispersal distance before reproducing, this allele would have travelled a maximum of eight home range diameters (2.2km) from M64 in three generations (Figure 12).

Figure 12. Movement of two rare alleles, 6PGD-150 and SER1-150, through the woodland study population.  $\rightarrow$  = carrier disappeared from study area. x = carrier died.



6PGD - 150



SER - 150

The other two rare alleles exhibited similar rates of gene flow. The AK1-180 gene was found in the subordinate male in M58, who had been born in neighboring troop M53; in the breeding male in troop M57 two home range diameters away from M53, and in two adult males of unknown paternity born in troop M62, 5.4 home range diameters away from M53. The allele in the last case apparently came from a common father who was no longer present in the troop at the onset of the study. One of these two males became the breeding male in M62 during 1978 (Rudran 1979), and in 1983 became the breeding male in neighboring troop M67, which is also 5.4 home range diameters away from M53. The second male invaded M67 also, but remained subordinate. The AK1-180 allele thus travelled a maximum of 5.4 home range diameters within the study population over a minimum of 13 years, or 2.6 generations. The SER1-150 allele was exhibited only within a single family line in M62: an adult female, her son, and her son's daughter. The old female died before producing more offspring, and the son became the breeding male in the neighboring troop. His daughter emigrated from the study area. This allele, which was presumably introduced into the population by the adult female, travelled only one home range diameter within the study population in 14 years (minimum age of her son at the end of the study). Assuming the granddaughter emigrated the mean distance for dispersing females before reproducing, the SER1-150 allele travelled six home range diameters (1.6km) in 14 years, or 2.8 generations (Figure 12).

The high level of population subdivision confirmed by  $F_{ST}$  values indicated that when subunits (troops) were pooled,  $F_{IT}$  would be inflated by Wahlund effect (Wahlund 1928). As expected, high  $F_{IT}$  values were

generally correlated with high  $F_{ST}$  values (Table 13) with the exception of the PEP-C locus in the gallery population, and were therefore able to give little information about correlation among gametes on a population-wide level. Both  $F_{IT}$  and  $F_{IS}$  values for variation between subpopulations (Table 14) reflect pooled data, and were likewise affected.

The correlation among gametes coming together within troops ( $F_{IS}$ ) was negative for almost all loci (Table 13), indicating an excess of heterozygotes within troops relative to the number expected by standard variance components predictions (Wright 1978). Allelic  $F_{IS}$  values for 6PGD, AK-1, ADA, GPI, PEP-D, and ME were consistently negative for troops in both populations, and for all troops combined. These values were significantly different from zero at AK-1, ADA, GPI, and PEP-D in both the woodland troops and combined troops. Allelic  $F_{IS}$  among gallery troops exhibited a somewhat different pattern than among woodland troops. Only ME had a significant negative value, and a positive correlation among gametes was found at loci PNP, SER-1, and PEP-C. Weighted mean  $F_{IS}$  values, however, were negative for both populations, as well as for combined troops. The bootstrap analysis demonstrated that the mean  $F_{IS}$  of 0.136 for combined troops was significantly different from that expected under random small grouping effects (Figure 13,  $p < .05$ ), indicating that negative correlation among uniting gametes in troops is associated with troop structure.

As expected, genetic variance among matrilineages was substantially larger than among troops ( $F_{ST} = 0.333$ ,  $\chi^2 = 47.433$ ,  $df = 24$ ,  $p < .005$ ).

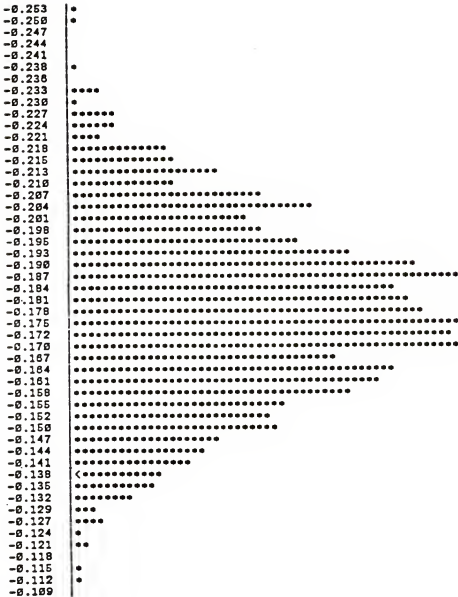


Figure 13. Histogram of bootstrap  $F_{18}$  results for troops within population. Probability that observed value of -0.136 does not differ from random grouping effects is less than 0.05.

On average, only 67% of the total genetic variability was present among the breeding females of any one troop. The bootstrap analysis indicated that random grouping of breeding females alone would not be expected to create this effect ( $p < .001$ ). Within any given troop then, breeding female gametes correlated due to relatedness within a matriline represented a reduced, non-random fraction of the variability present among population gametes as a whole. Application of the Wahlund principle to this distribution predicts that the number of heterozygotes resulting from pooling two or more population subunits (troops) should be directly proportional to the variance between them (Wahlund 1928). Thus the union of the gametes of a single male selected randomly from the population with those of a single matriline should produce an excess of heterozygotes in the first generation progeny. As the variance between gametes that come together increases, so should heterozygosis.

This can be demonstrated by comparing the F-statistics for troop breeding females only, troop offspring only, and troops (Table 15). Breeding females, as the single lineage products of such matings, exhibited the highest genetic variance between troops and also the highest level of heterozygosis ( $F_{IS} = -0.322$ ,  $p < .001$ ). Offspring only, which represent the related, multi-lineage products of such matings (more than one related mother and possibly more than one father), exhibited the second highest genetic variance among troops ( $F_{ST} = 0.247$ ,  $p < .001$ ), and also the second highest level of heterozygosis ( $F_{IS} = -0.264$ ,  $p < .001$ ). Troops, as a result of including one or more males originating from other lineages in the population (one of which contributes little or nothing to the troop gene pool), represented the



Table 15. Comparison of partitioning of genetic variance among different geneological subsets within the population. Asterisks refer to significance levels associated with chi-square values: \*\*\*p <.001.

	Troop Breeding	Breeding and Offspring	Complete Troops
$F_{IT}$	0.119	0.080	0.110
$F_{IS}$	-0.322 ***	-0.201 ***	-0.136 ***
$F_{ST}$	0.333 ***	0.234 ***	0.216 ***

largest sample of the total genetic variation of the three groups being compared. Genetic variance among troops was, accordingly, less than among offspring or adult females alone, as was the amount of excess heterozygosity.

#### Gene Frequency Change Over Distance

No evidence for clinal variation in gene frequencies was found. The dendrogram produced by the hierarchical cluster analysis is illustrated in Figure 14. The cophenetic correlation coefficient indicating goodness of fit between the dendrogram and the input matrix was 0.781. Woodland troops are prefixed with the letter "M" and gallery troops with the letter "G", with adjacent troops generally having consecutive numbers. As can be seen from the dendrogram, there appears to be wide discrepancy between troop genetic distance and geographic distance. Gallery troops G21 and G6, for example, cluster more closely with different woodland troops than they do with other gallery troops or with each other. Lack of agreement between geographic and genetic distances was confirmed by the Mantel test, in which no significant correlation was found between the geographic and genetic distance matrices ( $R = -0.028$ ;  $p > .44$ ).

Spatial autocorrelation at individual loci similarly reflected lack of association between geographic distance and directional gene frequency change. Correlograms based on Moran's coefficient are reported for each variable locus in Table 16. The upper class limits of each distance interval are indicated at the top of each column. No joins were possible between 2000m and 4000m, reflecting the gap between the woodland and gallery study areas that contained no troops.

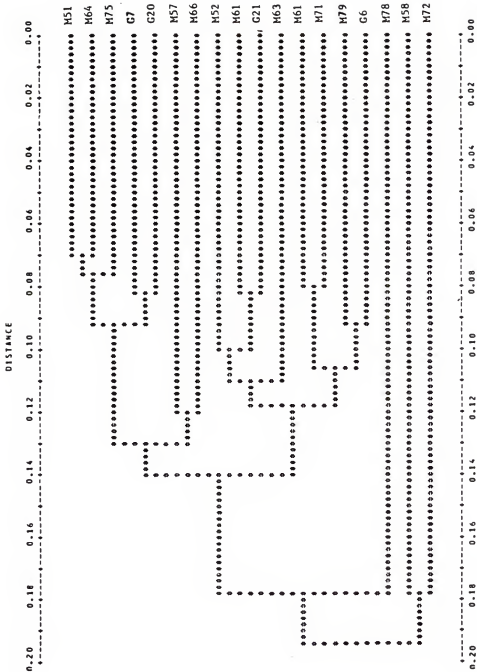


Figure 14. Dendrogram showing genetic distances among troops based on Rogers modified D.

Significance of individual coefficients is indicated by asterisks. No regular pattern of clinal gene frequency change is discernable for any locus except ME, which alternates between significant positive and negative values at approximately 1200m intervals. Locus 6PGD shows significant negative correlation between 500m and 1200m, as expected given the limited distribution of the second allele (see Figure 12). Five loci: 6PGD, PNP, PEP-3, PEP-4, and ME, show a monotonic decrease in association over the first three distance classes, while AK-1 and PRO-1 show the opposite pattern.

The distribution of Moran's I coefficients at each distance interval is plotted against the upper distance class limits in Figure 15, following the representation technique established by Sokal et al. 1986. The average values for each correlogram are connected by a line. With the exception of the first distance interval of 400m, there is a tendency for coefficients within 2000m to be negatively correlated, but there is no monotonic decrease in gene frequency association with distance. The slope between 800m and 2000m is in fact approximately zero. Coefficients fluctuate widely around zero at distance intervals from 4000m to 6400m, exhibiting a noise pattern created by divergent trends at each locus.

#### Discussion

Social barriers to gene flow in red howlers are capable of promoting substantial genetic differentiation among social groups. Comparison of these results to those reported for genetic divergence among geographic populations of other species (Table 18) indicates that the among troop  $F_{ST}$  for red howlers is higher than that found, for

Table 16. Correlograms for 9 variable loci based on spatial autocorrelation analysis using Moran's I coefficient.

Locus	Distance in meters											
	400	800	1200	1600	2000	4000	4400	4800	5200	5600	6000	6400
CHYD	0.12	-0.15 *	-0.20 *	-0.06	-0.23	0.10	-0.18	-0.05	-0.16	0.04	0.10	0.10
PNP	-0.01	-0.02	-0.11	-0.05	-1.00 **	0.31	-0.13	0.13	-0.53	0.60 *	-0.34	-0.16
AK	-0.21	-0.10	0.00	-0.05	0.35	0.02	-0.02	-0.03	0.11	0.18	-0.03	-0.60
ADA	-0.09	-0.16	0.20	-0.17	-0.32	0.36	0.01	0.02	0.07	0.10	-0.50	-0.26
GEI	-0.01	-0.12	0.11	-0.29	0.28	0.01	-0.41	0.53 *	-0.70 *	-0.16	0.41	-0.43
HRD-1	-0.04	-0.01	0.15	0.12	-0.01	-0.30	-0.30	-0.11	-0.09	-0.26	-0.61	0.37
PRP-3	0.24	-0.02	-0.64 *	-0.25	-0.10	-0.20	0.03	0.20	0.12	0.03	-0.01	-0.28
PRP-4	0.03	-0.12	-0.20	-0.06	-0.06	0.78 *	-0.23	-0.55 *	0.29	-0.07	0.65	0.19
ME	0.39 *	-0.17	-0.69 *	-0.20	0.30	0.92 *	-0.09	-0.06	-0.68 *	-0.22	-0.12	0.80 *
Mean	0.05	-0.10	-0.14	-0.11	-0.09	0.22	-0.15	0.01	-0.17	0.03	-0.05	-0.03

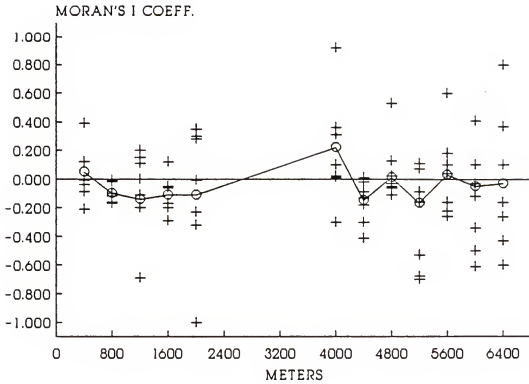


Figure 15. Distribution of Moran's I coefficients over geographic distance. Mean values averaged over loci are indicated by a circle and connected by line.

example, among moose populations in Scandinavia (Chesser et al. 1982), Japanese macaques on different islands in Japan (Kawamoto et al. 1985), and house mice on different farms in Texas (Selander and Kaufman 1975). Partitioning of genetic variance among red howler troops is compared to that found among social groups of other species in Table 17. Although genetic heterogeneity among howler troops is considerably higher than that observed among social groups of almost all species that have been examined, one can see that levels of genetic differentiation among social groups are generally comparable to those found among geographic demes. Genetic variance among marmot colonies (Schwartz and Armitage 1980), and vervet monkey troops (Dracopoli et al. 1983) for example, was similar to that found among geographic populations of rhesus macaques (Melnick et al. 1986), Scandinavian moose (Chesser et al. 1982), and California voles (Bowen 1982).

Despite these similarities, results from the howler study demonstrate that the partitioning of genetic variance among social unit demes can be radically different from that predicted by the various isolation by distance models designed for geographic demes (c.f., Marumaya 1969; Weiss and Kimura 1965; Wright 1978). The type of sampling error predicted for isolation by distance is fundamentally different from that exhibited by isolation via social structure. In isolation by distance models genetic variance among demes is determined by the amount of gene flow taking place between them, such that as migration among demes is reduced, genetic divergence is increased through drift. Low immigration into demes and a corresponding increase in consanguineous matings should result in an increase in correlation

Table 17. Genetic variability within and among social units in mammal species.

Species	Social units	Number of Loci	F <sub>st</sub>	F <sub>i</sub>	F <sub>it</sub>	References
Black-tailed prairie dog <u>Cynomys ludovicianus</u>	coterries within a colony	7	0.227	0.112	0.308	Chesser 1983
Pocket gopher <u>Thomomys bottae</u>	cluster groups within 2 fields	11	0.057	----	----	Patton & Feder 1980
Yellow-bellied marmot <u>Marmota flaviventris</u>	colonies within a region	8	0.070	-0.090	-0.070	Schwartz & Armitage 1980
Vervet monkey <u>Cercopithecus aethiops</u>	troops within a trapping locality	4	0.090	----	----	Dracopoli et al. 1983
Rhesus macaque <u>Macaca mulatta</u>	troops within a region	5	0.040	-0.085	-0.049	Melnick et al. 1984
Human	villages within a region	11 13 12	0.063 0.036 0.007	-0.012 -0.023 0.005	0.045 -0.009 0.015	Neel & Ward 1972
Red howler monkey <u>Alouatta seniculus</u>	troops within a locality	9	0.216	-0.136	0.110	present study



Table 18. Genetic heterogeneity among geographic demes in different species.

Species	Population unit	Number of Loci	$F_{st}$	Reference
Pocket Gopher <u>Thomomys bottae</u>	trapping localities within a state: California Arizona New Mexico	21	0.320 0.198 0.361	Patton & Yang 1977
California vole <u>Microtus californicus</u>	trapping localities within a region	4	0.050	Bowen 1982
House mouse <u>Mus musculus</u>	farms within Texas	4	0.174	Selander & Kaufman 1975
Fruit fly <u>Drosophila pseudoobscura</u>	local populations within the U.S.	10	0.030	Lewontin 1974
Brown land snail <u>Helix aspersa</u>	cities in California	6	0.162	Selander & Kaufman 1975
Human <u>Homo sapiens</u>	world-wide population	9	0.148	Cavalli-Sforza 1966
Crab-eating macaque <u>Macaca fascicularis</u>	islands in Indonesia	17	0.413	Kawamoto et al. 1985
Japanese macaque <u>Macaca fuscata</u>	islands in Japan		0.027	Kawamoto et al. 1985
Rhesus macaque <u>Macaca mulatta</u>	local populations throughout Asia	30	0.089	Melnick et al. 1986
Moose <u>Alces alces</u>	local populations within Scandanavia	5	0.096	Chesser et al. 1982

among gametes and a loss of gene diversity. Both genetic variance among demes ( $F_{ST}$ ) and correlation among gametes within demes ( $F_{IS}$ ) are thereby increased under conditions of genetic isolation.

Conversely, in genetic isolation induced by the social structure exhibited here, genetic variance among demes is determined by the amount of variance between male and female gametes within demes. Unrelated males mating within genetically divergent matrilineal increases the variance between uniting gametes within troops (and hence the  $F_{ST}$  value), but decreases correlation between uniting gametes within troops. This results in heterozygosity and a negative  $F_{IS}$  value. The degree of sampling error in this case will depend, as in the isolation by distance models, on the rate of immigration. As the number of immigrant males per generation increases, (1) relatedness among breeding females within troops, and corresponding consanguinity among female gametes, will be reduced due to a more diffuse paternal lineage; (2) male gametes will represent a larger sample of the total population genetic variability; and (3) variance between male and female gametes within and between troops will be reduced, accompanied by a lowered  $F_{ST}$  and a higher  $F_{IS}$ . Reduced relatedness among troop females caused by female immigration will have similar consequences. Unlike classic isolation by distance model predictions, therefore, genetic divergence among social demes mitigated by limited gene flow can be accompanied by relatively high levels of heterozygosity. Prout (1981) approached a similar conclusion based on a model of sex dependent migration, in which he predicted that excess heterozygosity should be directly proportional to the difference

between male and female immigration rates and the genetic variance among demes.

The manner in which these principles influence partitioning of genetic variance within socially structured populations can be illustrated by comparing the red howler results to those of the other social genetics studies that have been done (Table 17). Genetic variance among prairie dog coterries (Chesser 1983) and howler troops was several times higher than that exhibited among social units of the other species that have been studied. In fact, the among group  $F_{ST}$  value for these two species was of the same order of magnitude as that reported for different populations of pocket gophers in Arizona (Table 18: Patton and Yang 1977). Correspondingly, these are the only two of the species examined that have a social structure consisting of single male harems comprised of related females. Multi-male social units in which more than one male breeds such as marmots, rhesus macaques, and vervet monkeys, are genetically equivalent to single-male harems in which the male turnover rate is more than one per generation, as is possibly the case with pocket gopher cluster groups (Patton and Feder 1981). Harems in red howlers and prairie dogs are also the most likely to consist of single matriline. Social units in rhesus macaques, marmots, and vervet monkeys are typically composed of multiple related matriline, thereby reducing mean relatedness among females. While female immigration into social groups is very rare in howlers, prairie dogs, vervets, and rhesus macaques, average recruitment of females from outside the colony in marmots was as high as 50% (Schwartz and Armitage 1980). With the exception of the prairie dog study, reported  $F_{IS}$  values within social

groups were generally negative (Table 17). The amount of excess heterozygosity was correlated with the amount of genetic heterogeneity among social units in all cases except Yanomamo villages and prairie dog coterie.

#### Inbreeding and Heterozygosity

While both inbreeding and genetic variance between male and female gametes will increase  $F_{ST}$  among social groups, they will have opposite effects on the  $F_{IS}$ . No demographic information is available on the prairie dog populations reported in Chesser's study, but evidence from other studies suggests that the high level of correlation among gametes found within coterie may have resulted from inbreeding. Halpin (1986) observed that Chesser's colonies appeared similar to her study population with regard to degree of isolation from other colonies, and that this may have been responsible for similarly low dispersal rates between colonies. Immigration into her colony over a five year study period consisted of only three males, two of which she suspected had been born within the colony but had escaped trapping the year before. Males were able to maintain tenure in a single coterie for more than one generation, and there was no evidence that yearling daughters did not come into estrus when their father was present. Since 64%-95% of yearling males disappeared from the colony and those that remained did not reproduce until their second year, low immigration rate into colonies may have reduced male breeding competition to an extent that long term tenure and subsequent father-daughter matings were more often possible than not. Also, as Halpin observes, a male immigrating into a coterie that was born within another coterie in the same colony would be

likely to be a distant genetic relative of the females. Foltz and Hoogland's (1983) prairie dog study populations were in close proximity to other colonies. They reported a correspondingly high rate of inter-colony migration, and a negative within colony  $F_{IS}$  of  $-0.058$ . This value was not calculated in a manner compatible with the other  $F_{IS}$  values summarized in Table 17. It suggests, however, that correlation between gametes within prairie dog coterries under less isolated conditions may conform more to the pattern exhibited by other socially structured populations.

Although red howlers also exhibited a relatively high level of potential father-daughter mating, overall correlation between uniting gametes was significantly negative. The observation that males were occasionally able to inherit troops from their fathers, in conjunction with low male vagility between breeding attempts, suggests that indirect inbreeding with distant relatives may occur with some regularity. In fact considerable inbreeding may be necessary before a mean positive  $F_{IS}$  value is observed, depending on the degree to which other factors affecting variance between male and female gametes are promoted by the social organization in question. Mean coefficient of relatedness in Yanomamo villages, for example, has been calculated based on pedigrees to range between 0.3 and 0.5 (Neel 1978). Despite this high level of observed inbreeding, mean within village  $F_{IS}$  reported by Neel and Ward (1972) was  $-0.012$ . The  $F_{IS}$  value, however, was higher relative to the  $F_{ST}$  in the Yanomamo than in the other two Amerindian tribes (Table 17), suggesting that some increase in the  $F_{IS}$  was effected by inbreeding. This result is in agreement with the observation that within village

endogamy is higher in the Yanomamo than in the Makiritare or Xavante (Chagnon et al. 1970; Salzano et al. 1967; Smouse and Ward 1978). All three tribes practice a cross-cousin marriage system and, whenever possible, sororal polygyny (Chagnon 1983; Maybury-Lewis 1967; Ward and Neel 1970).

Negative  $F_{IS}$  values within socially structured populations have generally been interpreted as evidence for avoidance of inbreeding (e.g., Melnick 1986; Schwartz and Armitage 1980). Clearly, this is not the case. The significance of the  $F_{IS}$  for any social system can only be evaluated within the context of the appropriate demographic data, since other factors besides inbreeding can have a large effect on correlation between gametes.

#### Genetic Consequences of Social Group Formation

Another factor that will affect partitioning of genetic variance in a socially structured population is the manner in which new social groups are formed. With the exception of pocket gophers, which do not form cohesive social units (see below), red howlers are the only species listed in Table 17 in which new social groups are not formed through fissioning of larger groups along kin lines. Fissioning between genealogies should produce larger genetic differentiation among fission groups than random splitting ("lineal effect," Neel and Salzano 1967). This result has been demonstrated for fission of Yanomamo villages along patriline (Smouse et al. 1981), for division of toque macaque troops along matriline (Dittus 1986), and for division of rhesus macaque troops along matriline on Cayo Santiago Island (Mac Millan and Duggleby 1981; Olivier et al. 1981). Melnick and Kidd (1983), conversely, found

no evidence for lineal effect among fission groups in a population of rhesus macaques in Pakistan. They attributed this difference between the Pakistan and Cayo Santiago populations to the smaller matriline observed in Pakistan troops, and the smaller number of breeding males. Thus matrilineal fission groups in Pakistan would comprise a larger number of matrilines, among which offspring would be potentially more related through their fathers than their mothers.

It is clear, in any event, that formation of social groups through fission along kin lines can promote higher  $F_{ST}$  values among groups. The manner in which this has been presumed to occur is simply by increasing overall correlation among genomes within groups over that between groups (Melnick 1986; Neel and Salzano 1967; Olivier et al. 1981; Smouse et al. 1981). This explanation would necessarily incur an increase in the  $F_{IS}$  value as well, with the  $F_{IS}$  exhibited among matrilines being higher than that exhibited among whole troops. In fact, precisely the opposite pattern was observed in the howler population: the  $F_{IS}$  among matrilines was almost twice as negative as that among troops (Table 15). Genetic differentiation among matrilines was demonstrated to promote genetic divergence among troops by increasing the average variance between male and female gametes coming together within troops. Given the negative mean  $F_{IS}$  values within groups reported for the other species examined, and the similarities in their mating structure, it seems that this may be a more accurate explanation of the manner in which lineal fission effect generally operates.

This mechanism could be tested by comparing  $F_{IS}$  and  $F_{ST}$  values among matrilines to those among troops in species with similar patterns

of social organization. Olivier et al. (1981) examined  $F_{ST}$  values among troops, among matriline, and among natal segments of troops in the Cayo Santiago rhesus macaques. The relationship between these three factions was the same as that observed in the red howler population (Table 15). In the rhesus, the highest mean genetic heterogeneity was found among matriline ( $F_{ST} = 0.0789$ ), the next highest among natal segments ( $F_{ST} = 0.0204$ ), and the lowest among troops ( $F_{ST} = 0.0099$ ). The corresponding  $F_{IS}$  values were not reported. It would have been interesting to see how much the presumed increase in mean coefficient of relatedness among individuals due to the small, isolated nature of the colony limited the degree of variance between uniting gametes. So far,  $F_{IS}$  among matriline has been reported only for red howlers.

Since red howler troops do not form by fission, and founding females are not necessarily related to one another, a troop matriline develops gradually. In newer troops, breeding females will be less related to each other than in older troops. In growing populations, therefore, in which the rate of new troop formation is high, mean genetic differentiation among troops should be less than in a more stable population. This may have contributed to the lower  $F_{ST}$  and  $F_{IS}$  values observed among troops in the rapidly growing gallery population as compared to those observed in the woodland. Although population density in the woodland area was growing slowly prior to the 1981 sampling period (Table 11), this was mainly a result of existing troops increasing in size as opposed to new troop formation, such as was taking place in the gallery (Table 10).



In a population in which new troop formation takes place along kin lines, precisely the opposite pattern would be expected. A rapidly growing population with a high rate of new social group formation should exhibit greater mean genetic divergence among fission group kin lines than a steady state or slowly growing population in which groups are increasing in size. Mean relatedness among females in the Cayo Santiago rhesus macaque troops, for example, was higher in fission groups after splitting than in the troops which they comprised prior to splitting (Olivier et al. 1981). The lack of lineal effect between fission groups in the Pakistan rhesus population was attributed in part to a slow population growth rate resulting from high infant mortality, long interbirth intervals, and a short female lifespan, all of which limited the size to which female matriline within a troop could grow (Melnick and Kidd 1983).

#### Effective Population Size

At the social group level, effective population size per se is only important insofar as it is responsible for the degree of genetic variance between uniting gametes within the breeding units, since random loss of alleles through drift is not driving genetic divergence among groups. Effective population size among social groups is determined mainly by the number of females a single male can monopolize. Generally speaking, the larger the size of the group, the more breeding males there will be. This will decrease the variance between male and female gametes within social groups and increase the sex-ratio  $N_e$ . As has been demonstrated, however, only the former can be used to predict genetic heterogeneity among groups. A population consisting of large single

male harems should display greater variance between uniting gametes within social groups than a population consisting of small single male harems, and thereby exhibit greater genetic divergence among groups. A prediction based on sex-ratio  $N_e$  would demand the opposite conclusion.

Many mammal species, although not social, exhibit a mating system wherein several female territories lie within or adjacent to the territory of a single male who is able to effectively monopolize breeding access to the females (Eisenberg's type Ia mating system, Eisenberg 1981: e.g., pocket gophers, Patton and Feder 1981; black bears, Rogers 1974; many prosimians, Napier and Napier 1985). Furthermore, females in such systems are frequently matrilocal, occupying territories adjacent to their mothers and sisters (e.g., Rogers 1974; Sherman 1977). These expanded harems are genetically identical to those displayed by species that form cohesive social units. The same properties that govern partitioning of genetic variance among social groups should apply in these cases as well. Patton and Feder (1981) were able to demonstrate this effect in a population of pocket gophers.

#### Geographic Variation of Gene Frequencies

Gene flow among red howler troops was primarily of the type described by Kimura's (1953) stepping stone model. Although females dispersed much farther than from adjacent home range areas, they were unable to immigrate into established troops, thereby contributing very little to genetic exchange between them. The pattern in which rare alleles spread within the study area was commensurate with the highly localized character of observed gene flow. Both 6PGD-150 and SER1-150

were introduced into the woodland population by single females, but spread very slowly in a troop to troop fashion via dispersing males.

Although Endler (1977) has demonstrated that random drift combined with gene flow of the stepping stone type can generate clinal variation in gene frequencies, this effect was inhibited by low migration rates. High levels of genetic variation among demes fostered by low rates of gene flow, such as those displayed by howlers, were characterized by random fluctuations in gene frequencies that effectively swamped clinal effects (Endler 1977). In red howlers, this effect was enhanced by the fact that the immigrant potentially contributed one half the genetic complement of the troop to the succeeding generation. The dissimilarity in spatial autocorrelation patterns displayed by the various howler loci would be expected under these conditions. Lack of clinal variation in gene frequency change among howler troops was therefore attributable to the preeminence of stochastic perturbation over migration distance in determining different patterns of allele distribution. Sokal et al. (1986) reached a similar conclusion in explanation of low levels of genetic clinal autocorrelation observed among Yanomamo villages.

The genetic structure within howler populations imposed by the social organization had little effect on the rate of genetic divergence between geographic areas. Assuming that migration is balancing drift, and using Wright's island model formula

$$F_{ST} = 1 / (4 N m + 1)$$

(1969), the expected genetic differentiation between woodland and gallery populations based on the observed migration rate is  $F_{ST} = 0.019$ . This value is essentially indistinguishable from the observed  $F_{ST}$  of 0.021. Thus genetic divergence between geographic areas corresponded to the rate of gene flow between them in accordance with island model expectations.

Although within-troop heterozygosity can be maintained at higher levels than expected, the rate at which alleles are lost from populations remains dependent upon migration exchange. Overall, a far greater proportion of the total gene diversity was due to heterogeneity among troops (22%) than to geographic subdivision (2%). Similar results were found within and between populations of prairie dogs (Chesser 1983), rhesus macaques (Melnick et al. 1984), and vervet monkeys (Dracopoli et al. 1983).

#### Evolution of Socially Structured Populations

Social structure can impart a high degree of genetic divergence among social groups within populations in the absence of genetic isolation and inbreeding. Such populations are clearly not comprised of the inbred, isolated breeding units postulated to foster stasipatric speciation through fixation of chromosomal variants within groups (Bush 1975; Bush et al. 1977; Wilson et al. 1975). In circumstances, however, involving geographic isolation of small numbers of social groups such as colonizing situations, differences in the initial gene frequencies of founder populations may be larger than in division of a panmictic population, thereby engendering a higher likelihood of subsequent genetic divergence (Melnick 1986; Melnick et al. 1984; Templeton 1980).

Selection in a socially structured population such as that exhibited by red howlers may accelerate the rate at which a population can adapt to new areas. Structuring of populations into small, genetically heterogeneous demes can create interdemic differences in genetic variance that effectively expose a greater proportion of the genome to selection (Wright 1980). Individual troops displayed gene frequencies at various loci that diverged widely from the frequencies observed in the rest of the population. Interdemic selection in such a mosaic of genetic variation would result in more rapid spread of advantageous gene combinations than in a panmictic population, particularly in a colonizing situation. If troops vary genetically, and there is variation in troop reproductive success that is correlated with differences in gene frequencies, then the rate at which reproductively advantageous traits evolve will be proportional to the degree of genetic variation among troops for those characters (Wilson 1983).

Intertroop differences in reproductive success was a major component of howler population demography at Masaguaral. Competition for territory was observed to be particularly intense among new troops. Failure to establish adequate territory, long interbirth intervals, and high infant mortality all contributed to troop failure (see Chapter 3). Among the six new woodland troops that were established between December 1981 and February 1984, only three survived by July 1985, and one of the surviving troops, M82, had suffered almost complete infant mortality. Well established troops were also subject to failure. Troop M62 disappeared in 1982 due to female attrition, and M51 disappeared for unknown reasons during 1983. In all cases, new troops formed in the

vacated territories, and the ranges of adjacent troops expanded. Variation in male tenure length and troop reproductive success resulted in some troops consistently contributing larger numbers of offspring to the gene pool than others. Between the beginning of 1979 and mid 1985, for example, troop M77 produced 16 offspring that survived (i.e., either survived to dispersal age and left, or remained in the troop). Adjacent troop M76 with the same number of breeding females produced only 8 offspring during this same period. Furthermore, M77's offspring were all fathered by the same male, while M76 had experienced two male tenure changes during this time.

Intergroup differences in long-term reproductive success have been demonstrated in other primate populations. Using ten years of demographic data from a Cebus olivaceus population, Robinson (1988) demonstrated that the reproductive success of individual females, and the length of breeding male tenure, were significantly higher in large groups than in small groups. Mean troop size of the small groups was half that of the large groups, and remained constant over time. Large groups remained large, despite the splintering off of small fission groups. Small groups, apparently formed through the fission of subordinate matrilineal groups from large groups, remained small throughout the study. Large groups were dominant over small groups, independent of interaction locality, and were able to out-compete small groups by displacing them at feeding sites. This was postulated to contribute to the higher fecundity exhibited by the large group females. In the mantled howler (Alouatta palliata) population on Barro Colorado Island, 30 years of demographic data revealed that troops of nine to eleven

adults contributed nearly twice the proportion of total young to the population as smaller or larger troops, which ranged between 4 and 22 adults (Calhoun 1963). It is not clear, however, how much temporal variation in size was exhibited by individual troops.

Since red howler troop females and their daughters will always contribute half of the alleles born into every generation of a troop's lifetime, they will have the most enduring influence upon troop genetic configuration. In troop M72, for example, the frequency of the common ADA 100 allele is extremely low (Table 12). This is due mainly to the fact that three of the breeding females are homozygous for the uncommon ADA 125. The fourth, who died in 1986 (D. Rumiz, pers. comm.), was heterozygous. This troop will always produce offspring among which the frequency of the ADA 125 allele is higher than the population mean, regardless of the genotype of the breeding male. The probability of a new alpha male also being homozygous for the ADA 125 allele is about one in ten ( $q^2$ ), which is the approximate chance of fixation of this allele in M72.

The high level of mean heterozygosity exhibited by red howlers and the large genetic differences among troops may thus provide the means by which this species is able to adapt rapidly to new habitats, and thereby contribute to their ability to occupy the wide range of environmental conditions in which they are found. This may be particularly important with regard to utilizing new food resources containing an unfamiliar array of potentially harmful secondary compounds.

The success throughout Central and South America of the six species of howler that comprise the genus Alouatta may be due to social

and genetic factors similar to those outlined here for Alouatta seniculus. The large amount of chromosomal variation observed within and between species of Alouatta (Table 19) suggest that fixation of chromosomal variants in small, founder populations may have been an important element initiating speciation in this group. Such populations would be found frequently in a colonizing species. Evidence for this mechanism can be seen in the fixation of a translocation mutation in Alouatta palliata, in which the Y chromosome has become fused to autosomal pair B19 (Ma et al. 1975). Females have a diploid number of 54 chromosomes, while males have only 53. Only the A. palliata of Barro Colorado Island have been examined, leaving the degree of fixation of this mutation throughout the species yet to be determined.

Intraspecific variation in karyotype has been demonstrated for Alouatta seniculus (Yunis et al. 1976). Individuals captured in two localities on the east side of the Magdalena River in Colombia exhibited a pericentric inversion of chromosome 13, while those from the three localities on the west side did not. Red howlers, with only 44 chromosomes, appear to be the most derived of the four species that have been examined (Table 19).



Table 19. Comparative karyology of four *Alouatta* species.

Species	--- Autosomes ---						Reference
	2N	MC	SMC	AC	X	Y	
<i>A. seniculus</i>	44	10	6	26	AC	SMC	Bender & Chu (1963) Yunis et al. (1976)
<i>A. fusca</i>	50	4	16	28	SMC	AC	Koifmann & Saldanha (1974)
<i>A. caraya</i>	52	4	16	30	SMC	AC	Epozcue et al. (1968) Mudry-de-Pargament et al. (1975)
<i>A. palliata</i>	53 m 54 f	4	18	30	SMC	--	Ma et al. (1975)

AC = Acrocentric  
MC = Metacentric  
SMC = Sub-metacentric

## CHAPTER 5 CONCLUSION

Social barriers to gene flow are capable of promoting substantial genetic differentiation among red howler social groups over short geographic distances. The manner in which genetic divergence among social demes occurs, however, is fundamentally different from that predicted by isolation by distance models. In isolation by distance models, genetic variance among demes is determined by the amount of gene flow taking place between them, such that as migration among demes is reduced, genetic divergence is increased through drift. Both genetic heterogeneity among demes ( $F_{ST}$ ) and correlation among gametes within demes ( $F_{IS}$ ) are thereby increased. Conversely, under genetic isolation induced by the social system exhibited by red howler monkeys, unrelated males mating within genetically divergent matrilineal lines increases the variance between uniting gametes among troops (and hence the  $F_{ST}$  value), but decreases the correlation between uniting gametes within troops ( $F_{IS}$ ). Unlike isolation by distance model predictions, then, genetic divergence among social demes mitigated by limited gene flow can be accompanied by relatively high levels of heterozygosity of individuals relative to demes. Variance between male and female gametes within troops was promoted by an essentially single-male harem breeding structure, low rate of random exchange among troops of breeding males,

and a high degree of relatedness among troop females. These factors were influenced by intrasexual competition for limiting resources that were distributed differently for each sex. In those species in which social groups contain more than one adult male, or reduced relatedness among females due to retention of multiple matriline, variance between gametes will be reduced and genetic heterogeneity among troops will be lowered. Correlation among gametes ( $F_{IS}$ ) will be increased. The significance of the  $F_{IS}$  ("inbreeding coefficient") for any social system can only be evaluated within the context of the appropriate demographic data, since other factors besides inbreeding can have a substantial effect on correlation among gametes. Negative  $F_{IS}$  values obtained for populations subdivided into kin-oriented social groups must be interpreted with caution, and cannot be inferred as evidence for avoidance of inbreeding.

Genetic differentiation among social demes may influence the rate of genetic divergence among geographic areas by (1) promoting larger differences in the initial gene frequencies of founder populations and (2) accelerating the rate at which populations can respond to different selection regimes by exposing a larger proportion of the genome to selection via inter-group variation. Interdemic selection in such a mosaic of genetic variation could result in the more rapid spread of advantageous gene combinations than in a panmictic population, particularly in a colonizing situation. The rapid local adaptation made possible by these factors may have helped to promote the tremendous radiation that was responsible for the current geographic range of the genus Alouatta. The large amount of chromosomal variation observed

within and between species of Alouatta suggest that fixation of chromosomal variants in small, founder populations may have been an important element influencing speciation in this group.

## REFERENCES

- Altland, K., R. Hackler, and W. Knoche 1980. Double one-dimensional electrophoresis of human serum transferrin: A new high resolution screening method for genetically determined variation. Hum. Genet. 54:221-231.
- Altmann, S., S. Wagner, and S. Levington 1977. Two models for the evolution of polygyny. Behav. Ecol. Sociobiol. 2:397-410.
- Bateson, P. 1983. Optimal outbreeding. In: Mate Choice. P. Bateson, ed., Cambridge University Press, Cambridge. pp 257-277.
- Bekoff, M. 1977. Mammalian dispersal and the ontogeny of individual behavioral phenotypes. Am. Nat. 111:715-732.
- Bender, M.A., and E.H.Y. Chu 1963. The chromosomes of primates. In: Evolutionary and Genetic Biology of Primates, Vol. 1. J. Buettner-Janusch, ed., Academic Press, New York. pp 261-310.
- Bengtsson, B.O. 1978. Avoiding inbreeding: at what cost? J. Theoret. Biol. 73:439-444.
- Bischof, N. 1975. Comparative ethology of incest avoidance. In: Biosocial Anthropology. R. Fox, ed., John Wiley, New York. pp 37-67.
- Bjorndal, K.A. 1985. Nutritional ecology of sea turtles. Copeia 1985(3):736-751.
- Bowen, B.S. 1982. Temporal dynamics of microgeographic structure of genetic variation in Microtus californicus. J. Mammal. 63:625-38.
- Brown, J.L. 1987. Helping and Communal Breeding In Birds: Ecology and Evolution. Princeton University Press, Princeton, New Jersey.
- Bush, G.L. 1975. Modes of animal speciation. Ann. Rev. Ecol. Syst. 6:339-64.
- Bush, G.L., S.M. Case, A.C. Wilson, and J.L. Patton. 1977. Rapid speciation and chromosomal evolution in mammals. Proc. Natl. Acad. Sci. USA 74(9):3942-3946.

- Bygott, J.D., C.R. Bertram, and J.P. Hanby 1979. Male lions in large coalitions gain reproductive advantages. Nature 282:839-841.
- Calhoun, J.B. 1963. The social use of space. In: Physiological Mammalogy, vol. 1. V.M. Mayer and R.G. van Gelder, eds., Academic Press, New York and London. pp 1-64.
- Cavalli-Sforza, L.L., 1966. Population structure and human evolution. Proc. Roy. Soc. (London) Ser. B 164:362-379.
- Chagnon, N.A. 1983. Yanomamo: The Fierce People. Holt, Reinhart & Wilson, New York.
- Chagnon, N.A., J. Neel, L. Weitcamp, H. Gershowitz, and M. Ayres 1970. The influence of cultural factors on the demography and pattern of gene flow from the Makiritare to the Yanomamo Indians. Amer. J. Phys. Anthropol. 32:339-350.
- Cheney, D.L., and R. Seyfarth 1983. Nonrandom dispersal in free ranging vervet monkeys: Social and genetic consequences. Amer. Nat. 122:392-412.
- Chepko-Sade, B.D., and Z.T. Halpin 1987. Mammalian Dispersal Patterns: The Effects of Social Structure on Population Genetics. Univ. Chicago Press, Chicago.
- Chepko-Sade, B.D., W. Shields, J. Berger, Z. Tang Halpin, W. Jones, L. Rogers, J. Rood, and A. Smith 1987. The effects of dispersal and social structure on effective population size. In: Mammalian Dispersal Patterns: The Effects of Social Structure on Population Genetics. B.D. Chepko-Sade and Z.T. Halpin eds., University of Chicago Press, Chicago. pp 287-321.
- Chesser, R.K. in prep. The apportionment of gene diversity in socially structured populations.
- Chesser, R.K. 1983. Genetic variation within and among populations of the black tailed prairie dog. Evolution 37(2):320-331.
- Chesser, R.K., C. Reuterwall, and N. Ryman 1982. Genetic differentiation of Scandinavian moose Alces alces populations over short geographical distances. Oikos 39:125-130.
- Crockett, C.M. 1984. Emigration by female red howler monkeys and the case for female competition. In: Female Primates: Studies by Women Primatologists. M.F. Small, ed., Alan R. Liss, New York. pp 159-173.
- Crockett, C.M. 1985. Population studies of red howler monkeys (Alouatta seniculus). National Geographic Research 1(2):264-273.

- Crockett, C.M., and J. F. Eisenberg 1987. Howlers: Variations in group size and demography. In: Primate Societies. B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, and T. Struhsaker, eds., University of Chicago Press, Chicago.
- Crockett, C.M. and T. Pope 1988. Inferring patterns of aggression from red howler monkey injuries. Amer. J. Primatology 14:1-21.
- Crockett, C.M., and R. Rudran 1987a. Red howler monkey birth data I: Seasonal variation. Amer. J. Primatology 13:347-368.
- Crockett, C.M., and R. Rudran 1987b. Red howler monkey birth data II: Interannual, habitat, and sex comparisons. Amer. J. Primatology 13:369-384.
- Crockett, C.M., and R. Sekulic 1984. Infanticide in red howler monkeys (Alouatta seniculus). In: Infanticide: Comparative and Evolutionary Perspectives. G. Hausfater and S. B. Hrdy, eds., Aldine, New York. pp 173- 191.
- Crow, J.F., and M. Kimura 1970. An Introduction to Population Genetics Theory. Burgess Publishing Co, Minneapolis. pp 591.
- Daly, J.C. 1981. Effects of social organization and environmental diversity on determining the genetic structure of a population of the wild rabbit, Oryctolagus cuniculus. Evolution 35(4):689-706.
- Dawkins, R. 1979. Twelve misunderstandings of kin selection. Z. Tierpsychol. 51: 184-200.
- Dittus, W.P.J. 1988. Group fission among wild toque macaques as a consequence of female resource competition and environmental stress. Anim. Behav. 36(6):1626-1645.
- Dixon, K.R., and J.A. Chapman 1980. Harmonic mean measure of animal activity area. Ecology 61:1040-1044.
- Dobson, F.S., and W.T. Jones 1985. Multiple causes of dispersal. Amer. Nat. 126:855-858.
- Dracopoli, N.C., F.L. Brett, T.R. Turner, and C.J. Jolly 1983. Patterns of genetic variability in the serum proteins of the Kenyan vervet monkey (Cercopithecus aethiops). Am. J. Phys. Anthropol. 6:39-49.
- Duvall, S.W., I.S. Bernstein, and T.P. Gordon 1976. Paternity and status in a rhesus monkey group. J. Reprod. Fert. 47:25-31.
- Eddy W.F. 1977. A new convex null algorithm for planer sets from ACM. Transactions on Mathematical Software 3:370-400.

- Egozcue J., and M. Vilarasau de Egozcue 1968. The Somatic Chromosomes. In: Biology of the Howler Monkey (*Alouatta caraya*). Bibl. primat., No. 7. M. Malinow, ed., Karger, Basel/New York. pp 1-27.
- Eisenberg, J.F. 1980. Habitat, economy, and society: some correlations and hypotheses for the neotropical primates. In: Primate Origins and Human Evolution. I. Bernstein and E. O. Smith, eds., Garland Press, New York.
- Eisenberg, J.F. 1982. The Mammalian Radiations. University of Chicago Press, Chicago.
- Emlen, S.T., and L.W. Oring 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215- 223.
- Endler, J.A. 1977. Geographic Variation, Speciation, and Clines. Princeton University Press, Princeton.
- Foltz, D., and J. Hoogland 1983. Genetic evidence of outbreeding in the black-tailed prairie dog (*Cynomys ludovicianus*). Evolution 37:273-281.
- Gaines, M.S., and L.R. McClenaghan 1980. Dispersal in small mammals. Ann. Rev. Ecol. Syst. 11:163-196.
- Gallaher, R.N., C.O. Weldon, and J.G. Futral 1975. An aluminum block digester for plant and soil analysis. Soil Sci. Soc. Am. Proc. 39:803-806.
- Gaulin, S.J.C., and C.K. Gaulin 1982. Behavioral ecology of *Alouatta seniculus* in Andean cloud forest. Intern. J. Primatol. 3(1):1-32.
- Glander, K.E. 1975. Habitat and Resource Utilization: An Ecological View of Social Organization in Mantled Howler Monkeys. Ph.D. Dissertation, University of Chicago, Chicago.
- Glander, K.E. 1980. Reproduction and population growth in free-ranging mantles howler monkeys. Am. J. Phys. Anthropol. 53:25-36.
- Goering, H.K., and P.J. Van Soest 1970. Forage fiber analysis (apparatus, reagents, procedures and some applications). Agriculture Handbook No. 379. USDA, Washington, D.C.
- Golding, E.J., M.F. Carter, and J.E. Moore 1985. Modification of the neutral detergent fiber procedure for hays. J. Dairy Sci. 68:2732-2736.
- Greenwood, P.J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. Anim. Behav. 28:1140-1162.



- Halpin, Z.T. 1987. Natal dispersal and the formation of new social groups in a newly established town of black-tailed prairie dogs (*Cynomys ludovicianus*). In: Mammalian Dispersal Patterns: The Effects of Social Structure on Population Genetics. B.D. Chepko-Sade and Z.T. Halpin, eds., University of Chicago Press, Chicago. pp 104-118.
- Hamleton, L.G. 1977. Semiautomated method for simultaneous determination of phosphorus, calcium, and crude protein in animal feeds. J. Ass. Off. Agric. Chem. 60:845-852.
- Harcourt, A.H. 1978. Strategies of emigration and transfer by primates, with particular reference to gorillas. Z. Tierpsychol. 48:401-420.
- Harris, H., and D.A. Hopkinson 1977. Handbook of Enzyme Electrophoresis in Human Genetics. North-Holland Publ. Co., Amsterdam.
- Hauser, G. 1975. Dominance and reproduction in baboons. In: Contributions to Primatology, vol. 7. S. Karger, Basel.
- Itani, J. 1972. A preliminary essay on the relationship between social organization and incest avoidance in nonhuman primates. In: Primate Socialization. F.E. Poirer, ed., Random House, New York. pp 165-171.
- Jones, C.B. 1980. The functions of status in the mantled howler monkey *Alouatta palliata* Gray: Intraspecific competition for group membership in a folivorous, neotropical primate. Primates 21:389-405.
- Karlin, S., and R.B. Campbell. 1980. Polymorphism in subdivided populations characterized by major and subordinate demes. Heredity 44:151-168.
- Kawamoto, Y., T.M. Ishcack, and J. Supriatna. 1984. Genetic variations within and between troops of the crab-eating macaque (*Macaca fascicularis*) on Sumatra, Java, Bali, Lombok and Sumbawa, Indonesia. Primates 25:131-159.
- Kimura, M. 1953. "Stepping stone" model of population. Ann. Rept. Nat. Inst. Genet. Japan 3:62-63.
- Kimura, M., and G.H. Weiss 1964. The stepping stone model of population structure and the decrease of genetic correlation with distance. Genetics. 49:561-576.
- Koiffmann, C.P., and P.H. Saldanha 1974. Cytogenetics of Brazilian monkeys. J. of Human Evol. 3:275-282.
- Levene, H. 1949. On a matching problem arising in genetics. Ann. Math. Stat. 20:91-94.

- Li, C.C., and D.G. Horvitz 1953. Some methods of estimating the inbreeding coefficient. Amer. J. Hum. Genet. 5:107-117.
- Lloyd, L.E., B.E. McDonald, and E.W. Crampton 1978. Fundamentals of Nutrition. W.H. Freeman and Company, San Francisco.
- Loy, J.D. 1971. Estrous behavior of free-ranging rhesus monkeys (Macaca mulatta). Primates 12:1-31.
- Ma, N.S.F., T.C. Jones, R.W. Thorington, A. Miller, and L. Morgan 1975. Y-autosome translocation in the howler monkey, Alouatta palliata. J. Medical Primatology 4:299-307.
- MacMillan, C., and C.R. Duggleby 1981. Interlineage genetic differentiation among rhesus macaques on Cayo Santiago. Am. J. Phys. Anthropol. 56:305-312.
- McKenna, J.J. 1979. The evolution of allomothering behavior among colobine monkeys: Function and opportunism in evolution. Amer. Anthropol. 81:818-840.
- McClellan, T. 1982. Electrophoresis buffers for polyacrylamide gels at various pH. Analytical Biochemistry 126:94-99.
- Malecot, G. 1955. Decrease of relationship with distance. Cold Spring Harbor Symp. Quant. Biol. 20:52-53.
- Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Res. 27:209-220.
- Maruyama, T. 1969. Genetic correlation in the stepping stone model with non-symmetrical migration rates. J. Appl. Prob. 6:463-477.
- Maybury-Lewis, D. 1967. Akwe-Shavante Society. Clarendon Press, Oxford.
- Melnick, D.J. 1987. The genetic consequences of primate social organization: A review of macaques, baboons and vervet monkeys. Genetica 73:117-135.
- Melnick, D.J., Jolly, C.J., and K.K. Kidd 1984. The genetics of a wild population of rhesus monkeys (Macaca mulatta). I. Genetic variability within and between social groups. Am. J. Phys. Anthropol. 63:341-360.
- Melnick, D.J., and K.K. Kidd 1983. The genetic consequences of social group fission in a wild population of rhesus monkeys (Macaca mulatta). Behav. Ecol. Sociobiol. 12:229-236.

- Melnick, D.J., M.C. Pearl, and A.F. Richard 1984. Male migration and inbreeding avoidance in wild rhesus monkeys. Am. J. Primatol. 7:229-243.
- Moore, J. 1984. Female transfer in primates. Inter. J. Primatol. 5:537-589.
- Moore, J., and R. Ali 1984. Are dispersal and inbreeding avoidance related? Anim. Behav. 32:94-112.
- Mudry-de-Pargament, M.D., M.L. Labal-de-Vinuesa, O.J. Colillas, and S. Brieux-de-Salum 1984. Banding Patterns of Alouatta caraya. Rev. Brasil. Genet. 7(2):373-379.
- Neel, J.V. 1978. The population structure of an Amerindian tribe, the Yanomama. Ann. Rev. Genet. 12:365-418.
- Neel, J.V., and F.M. Salzano 1967. Further studies of the Xavante Indians. X. Some hypotheses-generalizations resulting from these studies. Am. J. Human Genet. 19:554-574.
- Neel, J.V., and R.H. Ward 1972. The genetic structure of a tribal population, the Yanomama Indians. VI. Analysis by F-statistics (including a comparison with the Makiritire and Xavante). Genetics 72:639-666.
- Nei, M. 1977. F-statistics and the analysis of gene diversity in subdivided populations. Ann. Human Genet. 41:225-233.
- Neville, M.K. 1972. The population structure of red howler monkeys (Alouatta seniculus) in Trinidad and Venezuela. Folia Primatologica 17:56-86.
- Nevo, E. 1978. Genetic variation in natural populations: patterns and theory. Theor. Pop. Biol. 13:121-177.
- Nishida, T. 1981. The social structure of chimpanzees of the Mahale Mountains. In: The Great Apes, D.A. Hamburg and E.A. McCown, eds., Benjamin/Cummings, Menlo Park, California. pp 73-121.
- Olivier, T.J., C. Ober, J. Buettner-Janusch, and D.S. Sade 1981. Genetic differentiation among matrilineal in social groups of rhesus monkeys. Behav. Ecol. Sociobiol. 8:279-285.
- Packer, C. 1979. Intertroop transfer and inbreeding avoidance in Papio anubis. Anim. Beh. 27:1-36.
- Packer, C., and A.E. Pusey 1982. Cooperation and competition in coalitions of male lions: kin-selection or game theory? Nature 296:740-742.

- Packer, C., and A.E. Pusey 1983. Male takeovers and female reproductive parameters: a simulation of estrous synchrony in lions (Panthera leo). Anim. Beh. 31:334-340.
- Parker, G.A. 1983. Mate quality and mating decisions. In: Mate Choice. P. Bateson, ed., Cambridge University Press, Cambridge. pp 141-164.
- Patton, J.L., and J.H. Feder 1981. Microspatial genetic heterogeneity in pocket gophers: non-random breeding and drift. Evolution 35:912-920.
- Patton, J.L., and S.Y. Yang 1977. Genetic variation in Thomomys bottae pocket gophers: Macrogeographic patterns. Evolution 31:697-720.
- Peto, R., M.C. Pike, P. Armitage, N.E. Breslow, D.R. Cox, S.V. Howard, N. Mantel, K. McPhearson, J. Peto, and P.G. Smith 1976. Design and analysis of randomized clinical trials requiring prolonged observation of each patient. I. Introduction and design. Br. J. Canc. 34:585-612.
- Peto, R., M.C. Pike, P. Armitage, N.E. Breslow, D.R. Cox, S.V. Howard, N. Mantel, K. McPhearson, J. Peto, and P.G. Smith 1977. Design and analysis of randomized clinical trials requiring prolonged observation of each patient. Br. J. Cancer 35:1 - 30.
- Pope, T.R., and C. Crockett in prep. Adult male cooperation as an adaptive response to population structure.
- Prout, T. 1981. A note on the island model with sex dependent migration. Theor. Appl. Genet. 59:327-332.
- Pusey, A.E., and C. Packer 1987. Dispersal and philopatry. In: Primate Societies. B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, and T. Struhsaker, eds., University of Chicago Press, Chicago. pp 227-240.
- Reisner, A.H., P. Nemes, and C. Bucholtz 1975. The use of Coomassie brilliant blue G250 perchloric acid solution for staining in electrophoresis and isoelectric focusing on polyacrylamide gels. Anal. Biochem. 64:509-516.
- Ridpath, M.G. 1972. The Tasmanian Native Hen, Tribonyx mortierii. I-III. CSIRO Wildl. Res. 17:1-118.
- Robinson, J.G. 1988. Group size in wedge-capped capuchin monkeys Cebus olivaceus and the reproductive success of males and females. Behav. Ecol. Sociobiol. 23:187-197.
- Rogers, L.L. 1974. Movement patterns and social organization of black bears in Minnesota. Ph.D thesis, University of Minnesota, Minneapolis.

- Rudran, R. 1979. The demography and social mobility of a red howler (Alouatta seniculus) population in Venezuela. In: Vertebrate Ecology in the Northern Neotropics. J.F. Eisenberg, ed., Smithsonian Institution Press, Washington, D.C. pp 107-126.
- Schwartz, O.A. and K.B. Armitage 1980. Genetic variation in social mammals: the marmot model. Science 207:665-667.
- Scott, N.J., A.F. Scott, and L.A. Malmgren 1976. Capturing and marking howler monkeys for field behavioral studies. Primates 17:527-533.
- Sekulic, R. 1981. The significance of howling in the red howler monkey (Alouatta seniculus). Ph.D. thesis, University of Maryland, College Park.
- Sekulic, R. 1982. Behavior and ranging patterns of a solitary female red howler (Alouatta seniculus). Folia Primatol. 38:217-232.
- Sekulic, R. 1983. Male relationships and infant deaths in red howler monkeys (Alouatta seniculus). Z. Tierpsychol 61:185-202.
- Selander, R.K. and D.W. Kaufman 1975. Genetic structure of the brown snail (Helix aspersa). I. Microgeographic variation. Evolution 29:385-401.
- Selander, R.K., M.H. Smith, S.Y. Yang, W.E. Johnson, and J.B. Gentry 1971. Biochemical polymorphism and systematics in the genus Peromyscus. I. Variation in the old-field mouse (Peromyscus polionotus). Univ. Texas Publ. 7103:49-90.
- Sherman, P.W. 1977. Nepotism and the evolution of alarm call. Science 197:1246-53.
- Shields, W.M. 1982. Philopatry, inbreeding, and the evolution of sex. State University of New York Press, Albany.
- Shields, W.M. 1987. Dispersal and mating systems: Investigating their causal connections. In: Mammalian Dispersal Patterns: The Effects of Social Structure on Population Genetics. B.D. Chepko-Sade and Z.T. Halpin, eds., University of Chicago Press, Chicago. pp 3-24.
- Sigg, H., A. Stolba, J.J. Abegglen, and V. Dasser 1982. Life history of hamadryas baboons: physical development, reproductive parameters and family relationships. Primates 23:473-487.
- Slatkin, M. 1976. The rate of spread of an advantageous allele in a subdivided population. In: Population Genetics and Ecology. S. Karlin and E. Nevo, eds. Academic Press, New York. pp 767-780.
- Smith, D.G. 1981. The association between rank and reproductive success in male rhesus monkeys. Am. J. Primatol. 1:83-90.

- Smith, R.H. 1979. On selection for inbreeding in polygynous animals. Heredity 43:205-211.
- Smouse, P.E., V.J. Vitzthum, and J.V. Neel 1981. The impact of random and lineal fission on the genetic divergence of small human groups: a case study among the Yanomama. Genetics 98:179-197.
- Smouse, P.E. and R.H. Ward 1978. A comparison of the genetic infrastructure on the Ye'cuana and the Yanomama: a likelihood analysis of genotypic variation among populations. Genetics 88:611-631.
- Smuts, B.B. 1985. Sex and Friendship in Baboons. Aldine, Hawthorne, New York.
- Smuts, B.B. 1987. Sexual competition and mate choice. In: Primate Societies. B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, and T. Struhsaker, eds., University of Chicago Press, Chicago. pp 385-400.
- Sneath, P.H.A., and R.R. Sokal 1973. Numerical Taxonomy. W.H. Freeman, San Francisco.
- Sokal, R.R., and N.L. Oden 1978. Spatial autocorrelation in biology. I. Methodology. Biol. J. Linn. Soc. 10:199-228.
- Sokal, R.R., and N.L. Oden 1978. Spatial autocorrelation in biology 2. Some biological implications and four applications of evolutionary and ecological interest. Biol. J. Linn. Soc. 10:229-249.
- Sokal, R.R., and I.L. Rohlf 1969. Biometry. W.H. Freeman and Company, San Francisco.
- Sokal, R.R., P.E. Smouse, and J.V. Neel 1986. The genetic structure of a tribal population, the Yanomamo Indians. IV. Patterns inferred by autocorrelation analysis. Genetics 114:259-287.
- Struhsaker, T.T. 1967. Behavior of vervet monkeys (Cercopithecus aethiops). University of California Publications in Zoology 82:1-64.
- Struhsaker, T.T. 1975. The Red Colobus Monkey. University of Chicago Press, Chicago.
- Sugiyama, Y. 1971. Characteristics of the social life of bonnet macaques (Macaca radiata). Primates 12:247-266.
- Templeton, A.R. 1980. The theory of speciation via the founder principle. Genetics 94:1011-1038.

- Terborgh, J. 1983. Five New World Primates. Princeton University Press, Princeton, New Jersey.
- Thorington, R.W., R. Rudran, and D. Mack 1979. Sexual dimorphism of Alouatta seniculus and observations on capture techniques. Vertebrate Ecology in the Northern Neotropics. J.F. Eisenberg, ed., Smithsonian Institution Press, Washington, D.C. pp 97-106.
- Troth, R.G. 1979. Vegetational types on a ranch in the central llanos of Venezuela. Vertebrate Ecology in the Northern Neotropics. J.F. Eisenberg, ed., Smithsonian Institution Press, Washington, D.C. pp 107-126.
- Vitousek, P.M. and R.L. Sanford 1986. Nutrient cycling in moist tropical forest. Ann. Rev. Ecol. Syst. 17:137-167.
- Wade, M.J. 1982. Group selection: Migration and the differentiation of small populations. Evolution 36:949-61.
- Wahlund, S. 1928. Zusammensetzung von populationen und korrelationsercheinungen vom standpunkt der vererbungslehre aus betrachtet. Hereditas 11:65-106.
- Ward, R.H., and J. Neel 1970. Gene frequencies and microdifferentiation among the Makiritare Indians. IV. A comparison of a genetic network with ethnohistory and migration matrices; a new index of genetic isolation. Am. J. Hum. Genet. 22:538-561.
- Waser, P.M., S.N. Austed, and B. Keane 1986. When should animals tolerate inbreeding? Amer. Nat. 128:529-537.
- White, J.D. 1968. Models of speciation. Science 159:1065-1070.
- Whittenberger, J.F. 1980. Group size and polygamy in social mammals. Amer. Nat. 115:197-222.
- Wilson, A.C., G.L. Bush, S.M. Case, and M.C. King 1975. Social structuring of mammalian populations and rate of chromosomal evolution. Proc. Natl. Acad. Sci. USA 72(12):5061-5065.
- Wilson, D.S. 1983. The group selection controversy: history and current status. Ann. Rev. Ecol. Syst. 14:159-87.
- Wilson, E.O., and W.H. Bossert 1971. A Primer in Population Biology. Sinauer, Sunderland, Massachusetts.
- Woolfenden, G.E., and J.W. Fitzpatrick 1986. Sexual asymmetries in the life history of the Florida Scrub Jay. In: Ecological Aspects of Social Evolution: birds and mammals. D.I. Rubenstein and R.W. Wrangham, eds., Princeton University Press, Princeton, New Jersey. pp 87-107.

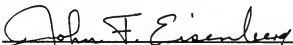
- Workman P.L., and J.D. Niswander 1970. Population studies on southwestern Indian tribes. II. Local genetic differentiation in the Papago. Am. J. Hum. Gen. 22:724-49.
- Wrangham, R.W. 1975. The behavioral ecology of chimpanzees in Gombe National Park, Tanzania. Ph.D. dissertation, Cambridge University, Cambridge, UK.
- Wrangham, R.W. 1980. An ecological model of female-bonded primate groups. Behavior 75:262-299.
- Wright, S. 1921. Systems of mating. II. The effects of inbreeding on the genetic composition of a population. Genetics 6:124-143.
- Wright, S. 1938. Size of population and breeding structure in relation to evolution. Science 87:430-431.
- Wright, S. 1943. Isolation by distance. Genetics 28:114-138.
- Wright, S. 1946. Isolation by distance under diverse systems of mating. Genetics 31:39-59.
- Wright, S. 1980. Genic and organismic selection. Evolution 34:825-842.
- Wright, S. 1965. The interpretation of population structure by F statistics with special regard to systems of mating. Evolution 19:395-420.
- Wright, S. 1969. Evolution and the Genetics of Populations. Vol. 2. The Theory of Gene Frequencies. University of Chicago Press, Chicago.
- Wright, S. 1978. Evolution and the Genetics of Populations. Vol. 4. Variability Within and Among Natural Populations. University of Chicago Press, Chicago.
- Yunis, E.J., O. Torres de Caballero, C. Ramirez, and E. Ramirez Z. 1976. Chromosomal variants in the primate Alouatta seniculus. Polia primatol. 25:215-224.



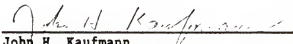
## BIOGRAPHICAL SKETCH

Theresa Pope grew up in San Leandro, California. She received a B.A. in zoology with honors from the University of California at Berkeley.


I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a thesis for the degree of Doctor of Philosophy.

  
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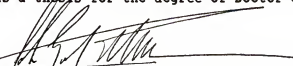
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